CHAPTER 3:
LOTIC METHODS AND INTER-YEAR VARIATION

FIELD METHODS

A total of 80 sample reaches were located along perennial streams within 20 watersheds (4 reaches/watershed). The selection of watersheds and reaches are described first, followed by a description of data collection at each sample reach.

Reach Selection

Watersheds

The arid climate of the basin affected the perennial nature of presumed perennial channels. I applied minimum size and mapped perennial channel length criteria to watershed selection: 1) no watersheds with a drainage area of less than 3 km^2 were considered for sampling because it was likely their flows were not perennial; and 2) perennial channels needed to be at least 3000 m in length to accommodate 4 sample reaches and have the upper-most reach located no closer than 500 m from the end of the mapped perennial channel. These criteria reduced the population of suitable watersheds within the basin from 53 to 34.

I constrained the selection of watersheds by orientation and disturbance, and then selected based on a random design. Orientation and disturbance represented the major environmental gradients in the basin at the watershed scale. Elevation and precipitation varied by orientation, and levels of disturbance varied considerably within the basin. Each of the 34 watersheds were assigned to 1 of the 4 major orientations: north, south, east, and west sides of the basin. Watersheds were also classified into one of 3 general disturbance classes (low, moderate, high), based on the proportion of the watershed occupied by various levels of development. I derived levels of development from a map of Recreation Opportunity Spectrum (ROS) classes (USDA no date) (Appendix 2). Three levels of disturbance were derived from the ROS classification: (1) undeveloped area with non-motorized access, (2) undeveloped area with motorized access, and (3) rural-urban development areas.

I selected watersheds randomly within each orientation by disturbance category, with at least one watershed selected within each category, for a total of 20 watersheds (Fig. 4, Appendix 1). Selection of watersheds resulted in a relatively equitable distribution across orientations and disturbance levels (Table 1).

TABLE 1. Watersheds selected for sampling in the Lake Tahoe basin. Numbers in parentheses reflect the number of watersheds determined to be available for sampling (based on sampling criteria) in the basin.

Basin orientation	Watersheds per disturbance class			Total no. of watersheds
	Low disturbance	Moderate disturbance	High disturbance	
N	2 (5)	1 (1)	1 (4)	4 (10)
E	3 (5)	1 (2)	2 (2)	6 (9)
S	2 (2)	2 (2)	1 (4)	5 (8)
W	2 (2)	2 (3)	1 (2)	5 (7)
Total	*9 (14)*	*6 (8)*	*5 (12)*	*20 (34)*

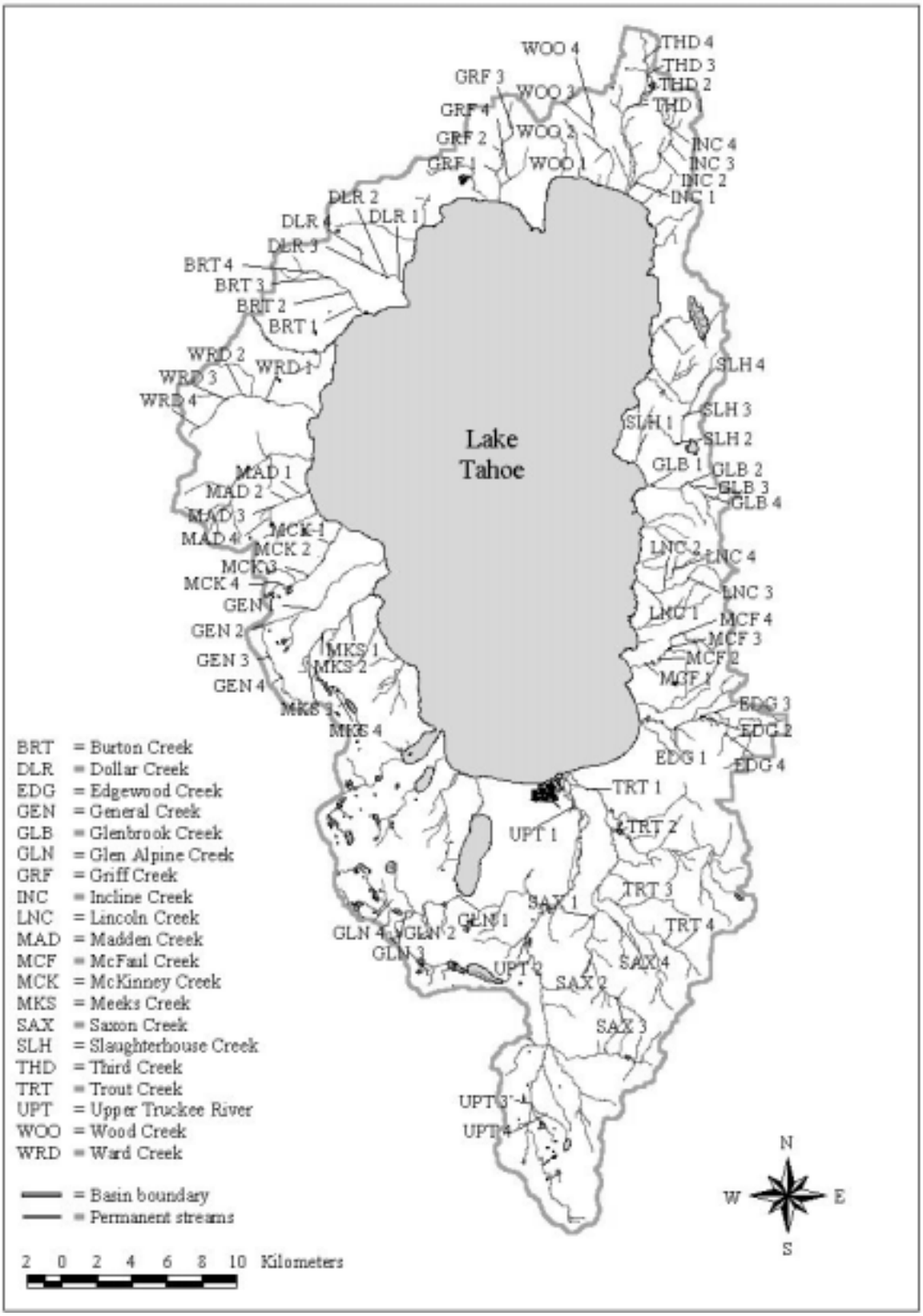

FIG. 4. Location of 20 watersheds and 80 reaches sampled in the Lake Tahoe basin, 1995 to 1996.

Reaches

Once watersheds were selected, four, 300 m reaches were located in each watershed. Reach location was constrained by watershed drainage area, headwater to mouth location, and disturbance. No tributaries in watersheds that drained less than 3 km^2 were considered for sampling because of the high probability of the stream being intermittent. Two watersheds (Griff and Saxon) had one tributary with an associated watershed above the minimum drainage size, and thus one reach was randomly located in each of these tributaries, with the remaining 3 reaches located along the main channel. In the remaining 18 watersheds, all 4 reaches were located along the main channel.

I constrained possible locations of main channel reaches by distance to channel mouth. I evenly divided the main channel into 3 or 4 sections (depending on whether 3 or 4 reaches were being located in the main channel) of equal length and then randomly located one reach in each section. Reaches were a minimum of 500 m apart to ensure independence of point count stations.

I post-stratified reaches by disturbance classes. The selected reaches had a relatively equitable distribution across orientation, disturbance and distance to channel mouth (Table 2).

TABLE 2. Reaches selected for sampling in each orientation and disturbance class within the Lake Tahoe basin.

Basin	Reaches per disturbance class			Total number
orientation	Low disturbance	Moderate disturbance	High disturbance	of reaches
N	5	6	5	16
E	8	9	7	24
S	5	10	5	20
W	5	8	7	20
Total	*23*	*33*	*24*	*80*

I chose reach length by reviewing existing data on channel morphology and calculating the average length of channel with consistent channel morphology. This average channel length was 300 m, and I therefore set reach length at 300 m to minimize variation in channel morphology within reaches. I established reaches in the field by locating the downstream end of the mapped reach, and then measuring out 300 m upstream in 25 m, straight line segments along bankfull channel.

The sample area consisted of the area within 30 m on either side of bankfull channel, for a sample area of 1.8 ha plus the channel itself. This sample area was selected based on the width of riparian associated vegetation in the basin, which was generally limited to within 30 m of the channel (based on visual estimates in the field).

All field sampling occurred over a 2-yr period. I sampled 32 reaches in 8 watersheds in 1995 and 48 additional reaches in 12 watersheds in 1996, for a total of 80 reaches in 1995 and 1996 (Appendix 3). Additionally, in 1996 I resampled one randomly selected reach from each watershed sampled in 1995. These data were used to analyze inter-year variation (see Chapter 3) and as part of the 1996 data set used to analyze invertebrates (see Chapter 7). All field sampling occurred from May through October.

The 8 reaches sampled in both 1995 and 1996 provided an indication of the variability introduced into the data set by annual differences introduced by weather and observers. Watersheds and reaches were selected using a stratified random design, with the stratification based on basin orientation and disturbance. Basin orientation and disturbance represent primary environmental gradients in the basin. One reach was randomly selected from each of the 8 watersheds sampled in 1995 (Table 3). Four methods were repeated in 1996: point counts, pitfall trapping, sweepnet sampling, and riparian searches.

TABLE 3. Stream reaches selected for inter-year comparison of riparian biota in the Lake Tahoe basin.

Watershed	Reach	Basin orientation	Disturbance rank	Distance to mouth
Burton	4	S	2	1244
Griff	4	S	2	378
McFaul	3	W	1	814
Meeks	4	E	1	2240
Saxon	4	N	2	800
Slaughterhouse	1	W	2	145
Third	4	S	1	2625
Ward	2	E	2	1353

Eleven observers in 1995 and 14 observers in 1996 were involved in field sampling. Four observers collected data in both years, for a total of 21 observers across both years (Appendix 4). The large number of observers introduced an unquantified amount of observer variability into the data. Within each year, observer assignments were arranged to maximize the number of different observers collecting data at each reach and within a watershed. This approach spread observer variability across all reaches and watersheds to the extent possible. In addition, data collection was preceded by extensive training periods where observers trained together on each sampling protocol for approximately 4 weeks, plus a 2 day refresher on each technique before data collection effort began.

Environmental Sampling

The environment was sampled to provide data on characteristics shown to be associated with the biological diversity of many taxonomic groups. The environmental characteristics I chose to sample are considered macro- and meso-scale environmental variables that affect most biota. I did not sample micro-scale environmental variables, such as soil moisture, air temperature, litter depth, or foliage volume. These features can be strong explanatory variables for population characteristics (e.g., abundance, survival, reproduction), but they tend to be taxa specific, and it was beyond the scope of this effort to address environmental variables associated with population-level effects. Macro-scale environmental variables, such as climate and aspect, and meso-scale environmental variables, such as vegetation and channel characteristics, constituted an appropriate match to the biological data in terms of the spatial grain and extent of their composition, structure, and associated processes (see Wiens 1989, O'Neill and King 1998). Admittedly, some explanatory power for individual measures of biological diversity may be lost by using one set of environmental variables for all biota, however it was a necessary sacrifice to enable the comparison of observed environmental relationships across taxonomic groups. It also served as a test of the ability of one set of environmental variables to serve as explanatory variables for many taxonomic groups.

Abiotic Environment

Two abiotic parameters were described in the field (elevation and aspect), and 2 were described using existing data (precipitation) and maps (basin orientation). Observers determined elevation in the field with an altimeter and double checked their readings with 1:24,000 scale topographic maps. Aspect was determined based on compass readings taken at 10 m intervals along the entire length of the channel (see channel mapping below). Precipitation data were obtained from summaries of precipitation data over the past 50 years (TRPA and USDA 1971, Daly 1995, Daly and Johnson 1999). Precipitation data used for analysis were in the form of a

published isocline map of the entire basin at the 1:100,000 scale (TRPA and USDA 1971), and these data were verified using more recent but unpublished digital data available from Oregon State University (Daly 1995). Basin orientation pertained to the location of a watershed within the basin as described by one of 4 cardinal directions.

Channel Characteristics

Channel characteristics were described in part by mapping the channel in 10-m increments along the entire length of the reach. Two observers used a fiberglass tape to measure off 10-m straight line increments along one bank. Observers determined the direction of each 10-m length of tape with a compass. In addition, at every 10-m interval, the width of the stream at bankfull was recorded. The resulting data provided a map of the channel. Percent slope of the channel was recorded at 3 locations along the reach (100 m, 200 m, and 300 m) using a clinometer. This technique provided a coarse estimate of stream gradient because the clinometer reading can easily vary by both observer and reading by at least a couple of percentage points.

Vegetation Characteristics

All vegetation data were collected in the field. The composition of vegetation communities and structural characteristics of the vegetation were described within each sample reach. Thirteen observers were involved in collecting vegetation data (Appendix 4). All 13 observers were also involved in riparian searches, and received intensive training in plant identification. In addition, observers trained together for multiple days to calibrate their identification of vegetation types.

I mapped the extent and location of each vegetation type occurring within sample reaches (30 m from bankfull channel on each side of the channel). Observers visually classified vegetation types based on the dominant species, and estimated the spatial extent of each vegetation type on a rectangular, blank grid map at a scale of approximately 1:1575 (1 cm = 1575 cm). The minimum mapping unit was 5 m^2.

Vegetation types were defined as those major vegetation series (classification of plant species associations established through statistical analysis) and habitats (associations that share relatively homogeneous environmental conditions) described by The California Native Plant Society (CNPS) (Sawyer and Keeler-Wolf 1995) (Appendix 5). Observers also recorded the dominant species for each vegetation type mapped as a cross-check of their classification in the field.

Vegetation structure was described by vegetation canopy cover, snags and logs in the sample reach, and logs in the channel. Observers used a spherical, convex densiometer (Lemmon 1956, Nuttle 1997) to provide an index of vegetation canopy cover. Observers took 4 densiometer readings (one in each cardinal direction) at each of 4 locations along the channel: 0 m, 100 m, 200 m, and 300 m. Observers recorded the number of dots covered and then calculated an average percent cover as a relative measure of cover.

I described snags and logs within the sample reach along three, 50-m transects located randomly within 3, 100-m segments along the stream (Fig. 5). One transect was located in each 100-m segment; the side of the channel on which it was located was randomly chosen. Snag and log surveys along each transect were conducted according to a standardized protocol developed and employed by the U. S. Forest Service (USDA 1997). Transects were established by laying out a 50-m, fiberglass tape. Observers laid out the transect approximately 15 m from bankfull channel, randomly locating the starting point between 0 and 50 m from the beginning of the segment. Observers recorded all snags > 0.3 m tall. Observers recorded snags $\geq$ 12 and $\leq$ 50 cm in diameter at breast height (dbh) within 5 m of the transect ($\cong$ 0.05 ha plot) and snags > 50 cm dbh within 10m of the transect ($\cong$ 0.10 ha plot). For each snag, observers recorded the following information: species, distance from transect, dbh (measured to the nearest cm using a Biltmore stick) (Avery and Burkhart 1983), height (measured to the nearest 0.5 m using a clinometer), and decay class (1-9). Decay classes used for snags followed Maser et al. (1979) (Appendix 6).

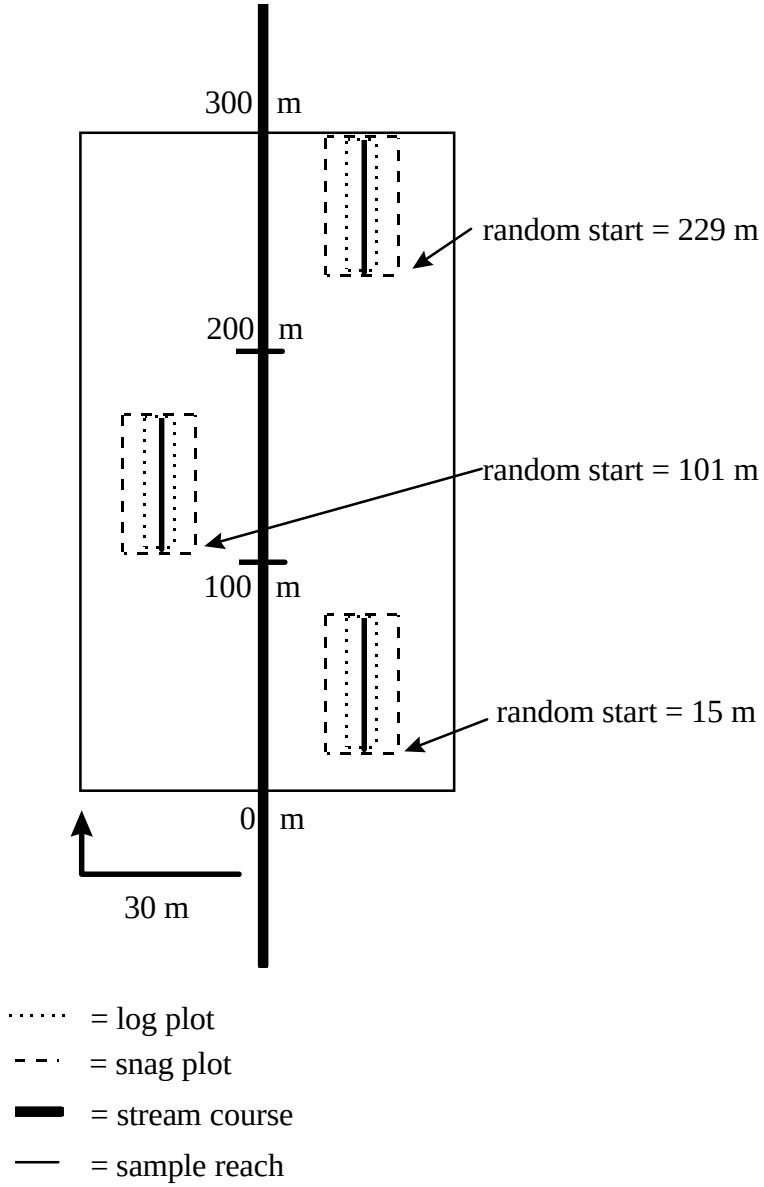

FIG. 5. Snag and log transects sampled in the Lake Tahoe basin.

Observers also recorded all logs longer than 1 m and wider than 25 cm at the large end along each transect. Logs > 25 cm and $\leq$ 50 cm in diameter at the large end were recorded within 5 m of the transect ($\cong$ 0.05 ha plot). Logs $\geq$ 50 cm at the large end were recorded within 10 m of the transect ($\cong$ 0.10 ha plot). For each log, observers recorded the following information: species, distance from transect, small and large diameter (measured to the nearest cm using a Biltmore stick), length (measured to the nearest 0.5 m with a Biltmore stick), and decay class (1 to 5) (Appendix 6). Decay classes for logs followed Reade (1985).

I also described large woody debris within bankfull channel for each 100 m segment. Large woody debris was defined as all pieces of wood greater than 10 cm diameter at the large end and at least 1 m long (Ruediger and Ward 1996). Observers measured diameter and length using a Biltmore stick. Observers recorded the following information for each piece of woody debris: species, diameter at the small and large ends (to the nearest cm), length (to the nearest 0.5 m), decay class (1-5) (Appendix 6) and whether the log was suspended. A log was considered suspended if over 50% of the log was suspended above bankfull. If observers encountered a large aggregation of woody material, they estimated the volume of the aggregation in lieu of describing each individual woody piece. An aggregation was defined as 3 or more pieces of woody debris touching each other. Observers estimated volume by recording each of the 3 dimensions to the nearest 0.5 m.

Disturbance Characteristics

I described disturbance within 250 m (6.25 ha area) of the center of each reach within which the proportion of the area occupied by ground disturbance was quantified by consulting 1997 1:8000 aerial photos and calculating area disturbed using with dot grids. A distance of 250 m was selected because it encompassed all biological and environmental data collection efforts associated with each reach and described the level of disturbance in the vicinity of the reach. The 250 m distance offered a representative and independent measure of disturbance for each reach.

Biological Sampling

Biological sampling at the reach scale consisted of sampling vertebrates, invertebrates, vascular plants, and fungi. I used a variety of techniques to describe the presence and abundance of biota. Each sampling effort is described in detail below. The number and training of observers is also described. Taxonomic and methods specialists (e.g., professional lichenologists, botanists, ornithologists) from a variety of institutions and knowledgeable of the Sierra Nevada or the Lake Tahoe basin were employed in the training of field personnel.

Point Count Sampling

I sampled birds and Douglas squirrels (*Tamiasciurus douglasii*) by conducting 8 point counts in and around each 300 m sample reach (Fig. 6). Although point count methodology was primarily designed for counting birds, it is an effective technique for counting squirrels (e.g, Sieving and Willson 1998), particularly Douglas squirrels, since their vocalizations are unique and frequent. The 8 point count stations were spaced 200 m apart, with 4 points located along the channel and 4 points located upslope on either side of the center 2 points along the channel. Previous studies have found that approximately 99% of all detection occur within 125 m of the observer (Ralph et al. 1993). Point count stations intended to characterize one location, such as a reach, are often placed much closer together (Ralph et al. 1993). I placed point count stations 200 m apart to minimize double counting between stations and yet place stations such that they characterized bird assemblages in the vicinity of stream reaches.

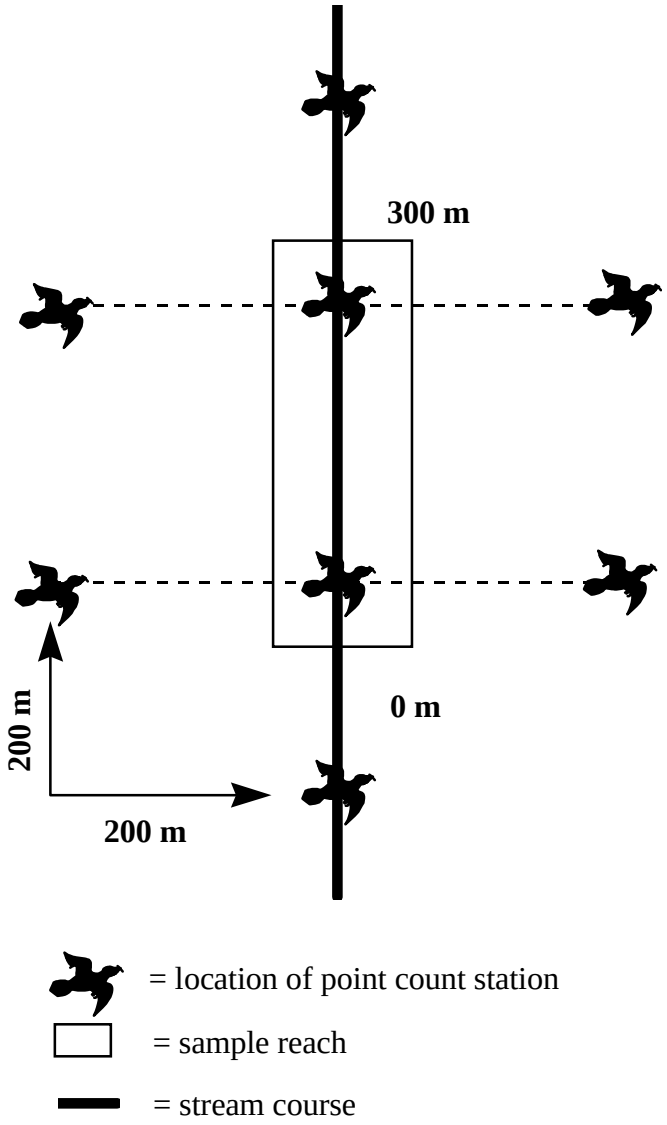

FIG. 6. Location of point count stations at each reach in the Lake Tahoe basin.

During counts, observers recorded all vertebrates seen or heard. As such, counts had an unlimited distance. Point counts are typically conducted from 5 to 10 min, depending on the circumstance (e.g., Dawson et al. 1995, Lynch 1995, Thompson and Schwalbach 1995). I conducted counts for a 10-min period to facilitate a more complete accounting of the bird species at each point (and reduce detectability biases that may have occurred as a result of different vegetation types and stream sizes). Observers conducted counts between 0530 and 0930 hrs, and began no sooner than 15 min after official sunrise. Observers waited at least 1 minute after arriving at a point before beginning the count to allow the birds to settle down. Observers did not conduct counts if it was precipitating or if the wind was stronger than a slight breeze.

Observers conducted counts between May 20 and August 14, with the majority (81%) of counts occurring in June and July. The latest dates were associated with the highest elevation reach sampled, and it was sampled in 1995 which was a longer winter with higher precipitation than the winter of 1996. Sample dates corresponded closely between years (Fig. 7). Timing of snow melt and chronology of breeding varied with elevation within the basin, with higher elevation sites being one to several weeks later compared to lower elevation sites. Lower

elevation sites became relatively snow-free from late May to mid June, while the upper most elevation sites were snowbound until early or mid July. In an attempt to synchronize the chronology of samples among reaches, counts started at low elevation reaches with eastern orientations, where snow melted the earliest, and proceeded upward in elevation and west in orientation over time. I sampled each reach 3 times over a 4-week period. A total of 9 observers conducted the 1920 point counts (80 reaches, 8 count stations per reach, 3 visits per station) (Table 1, Appendix 4). Point count data can be sensitive to observer bias (Raitt 1980). Four observers were common to both sample years, and these 4 observers conducted approximately 65% of the point counts in each year. All observers in both years trained together for 3 weeks before data collection began, increasing the uniformity of the data collection within and among years.

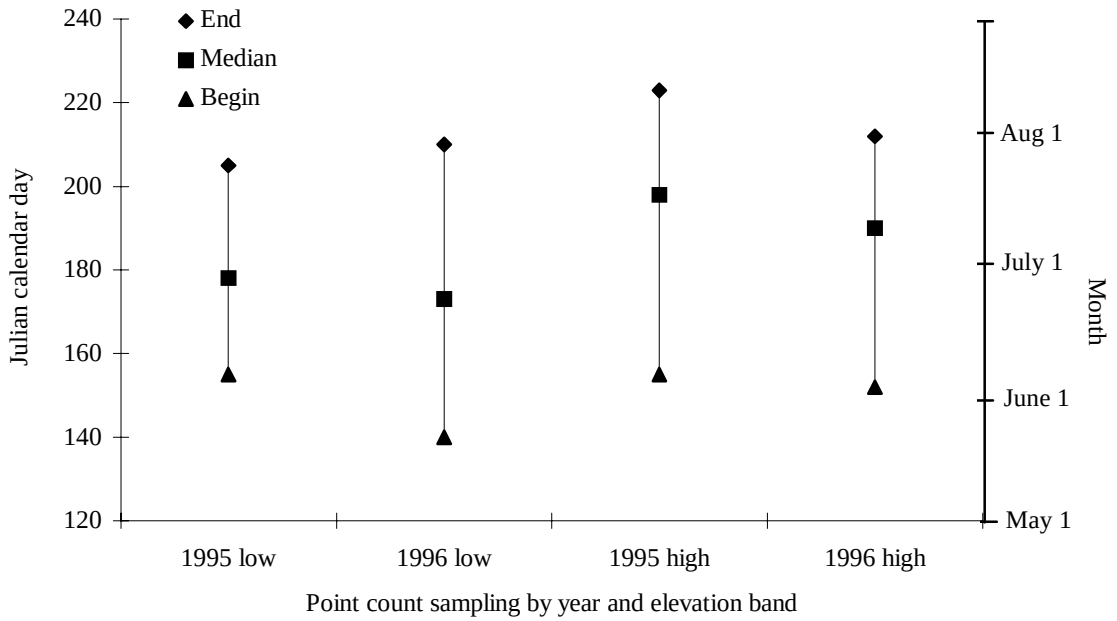

FIG. 7. Point count sample periods by year and elevation band. Reaches were grouped into 2 elevation bands: low (< 2100 m) and high (≥ 2100 m). Data were collected in the Lake Tahoe basin, 1995 to 1996.

Sampling dates in 1996 on the 8 resample reaches coincided closely with those in 1995 (Table 4). For the 8 resample reaches, a total of 9 observers collected the data (5 observers in 1995; 7 observers in 1996), with 3 observers collecting data in both years (Appendix 4).

TABLE 4. Point count sampling dates in 1995 and 1996 on 8 sample reaches in the Lake Tahoe basin. The dates span the 3 sample visits per reach.

Reach	1995 Samples	1996 Samples
Burton 4	June 30 - July 10	June 29 - July 21
Griff 4	June 14 - June 28	May 24 - July 2
McFaul 3	June 9 - June 26	May 28 - July 4
Meeks 4	July 12 - July 28	July 19 – August 1
Saxon 4	June 12 - June 30	May 24 - June 7
Slaughterhouse 1	June 6 - June 29	May 24 - June 28
Third 4	July 31 - August 14	July 22 – August 5
Ward 2	July 12 - July 25	June 10 - July 10

Small Mammal Trapping

I sampled small mammal species with Sherman live traps (7.6 x 8.9 x 30.5 cm) (Sherman Traps Inc., 3731 Peddie Dr., Tallahassee, Florida). Sherman traps have been shown to be an effective type of trap for most small mammal species when compared with snap traps (Sealander and James 1958) and they have the advantage of not removing individuals from the population. I used the long version of the standard 7.6 by 8.9 cm trap because it is designed to capture larger or longer-tailed small mammals. I wanted to capture as wide a variety of species as possible. Slade et al. (1993) showed that rates of capture of some species were higher, species were captured with equivalent frequency, and death rates were lower in longer compared to shorter-length (22.9 cm) traps.

I baited traps with rolled oats, whole oats, and sunflower seeds and added polyester fiberfill in the back of the trap to provide warmth. A combination of grains and nuts has been shown to be attractive to a wide variety of species (Beer 1964). The high fat content of nuts is also likely to help sustain animals caught in traps overnight in cold weather.

A grid of 108 traps was centered on each 300-m sample reach (Fig. 8). The grid consisted of 6 transects, 3 on each side of the channel. Transects were roughly parallel to the channel and located 5, 20 and 35 m from bankfull channel. Each transect consisted of 18 traps spaced 15 m apart starting at the 15 m mark of the reach, for a total of 108 trap stations. Observers set traps by 1600 hrs on day 1, checked them in the morning and evening for 3 days, and removed them the evening of the third day, for a total of 3 days and nights of trapping. All animals captured were identified to species, weighed, measured (total length, ear length, and other diagnostic characteristics), marked (by cutting a 1 cm patch of fur on the back just above the tail), sexed, examined for breeding status, and released at the trap site.

I conducted trapping between July 9 and September 9, in 1995 and 1996, starting at lower elevation and easterly orientation sites and moving upward in elevation and west in orientation over this 2-month period (Fig. 9). Sampling was conducted during the same general period between years, with only 1 to 2 days difference in the median trap date between years within each of 2 elevation bands (< 2100 m and ≥ 2100 m).

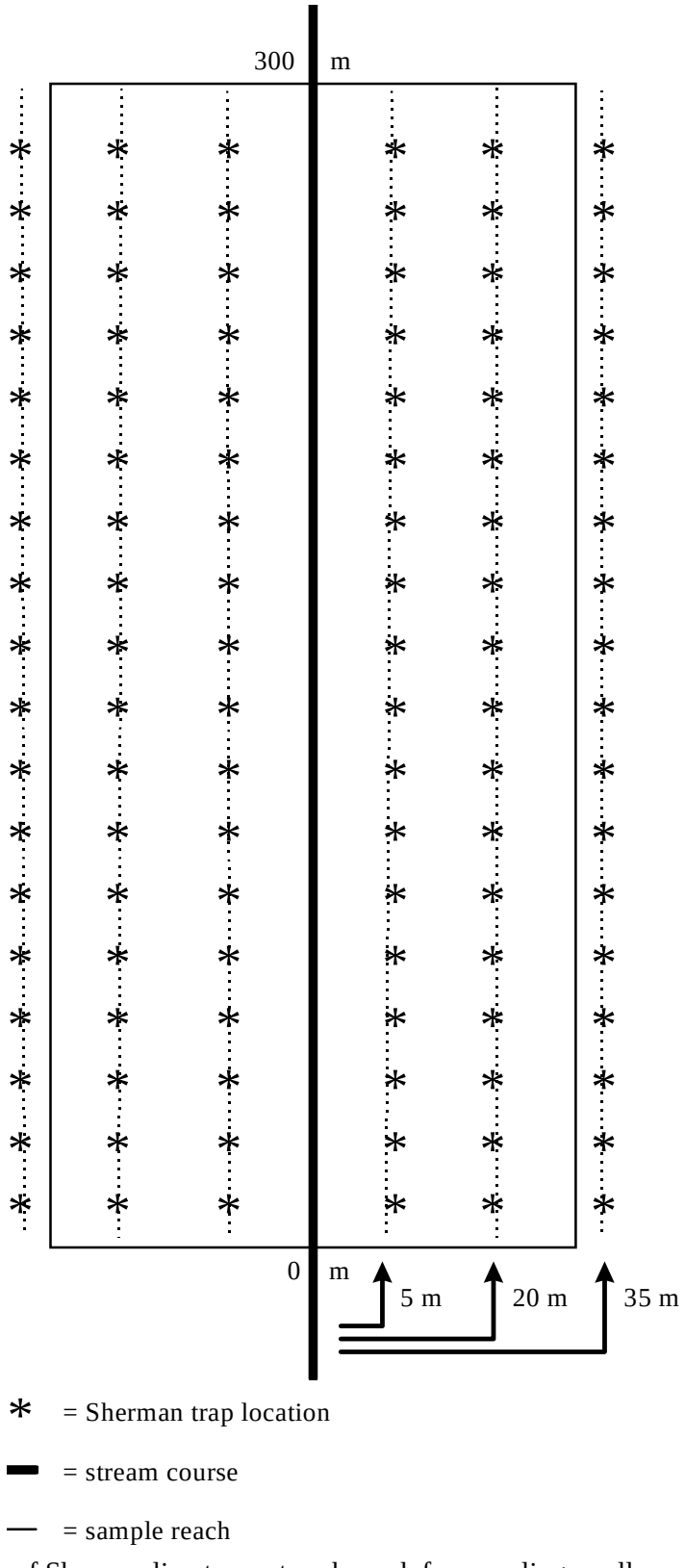

FIG. 8. Location of Sherman live-traps at each reach for sampling small mammals in the Lake Tahoe basin.

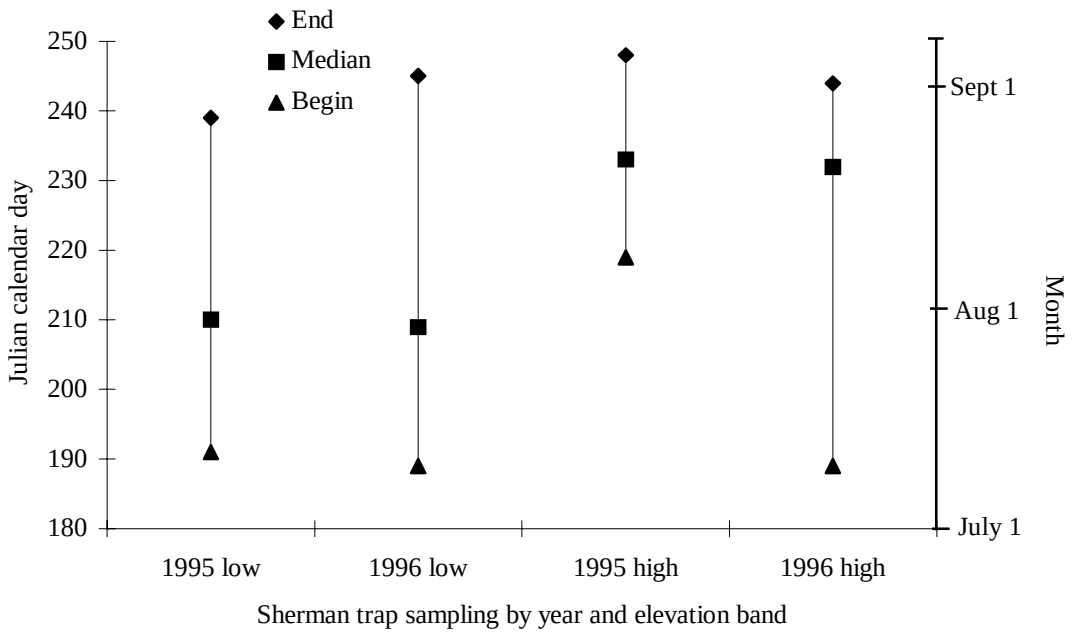

FIG. 9. Sherman trap sampling dates by year and elevation band. Sample reaches were divided into 2 elevation bands: low (< 2100 m) and high (≥ 2100 m). Data were collected in the Lake Tahoe basin, 1995 to 1996.

A total of 20 observers were involved in data collection over the 25,920 trap nights (80 reaches, 3 trap nights per reach, 108 traps each night). Four observers were common to both years. Training consisted of studying species identification through books, museum specimens, and voucher specimens collected during the study, and learning trapping and handling methods by conducting field trials for a 2-week period. The same 1 or 2 observers collected the data over the 3 trap nights at a given reach and observer pairs were mixed.

Pitfall Trap Sampling

I established pitfall trap transects on each reach. Pitfall traps target ground-moving insects and are recognized as a relatively efficacious method for identifying composition if insects die soon after they enter the trap and the trap does not overflow (Southwood 1978, Pedigo 1996, Weeks and McIntyre 1997).

A total of 20 pitfall traps were established per 300 m reach (Fig. 10). I arranged the traps in a grid of 4 transects. I placed 2 lines of 5 traps spaced 15 m apart 5 and 10 m from bankfull on each side of the channel. Pitfall traps consisted of a 9 cm wide by 14 cm tall (32 oz) outer plastic cup with a 9-cm wide by 11-cm tall (16 oz) inner plastic cup liner inside. Each liner cup had approximately 3 to 4 cm of soapy water in the bottom which served to retain and quickly kill individuals captured in the traps. Covers were intended to deflect rainfall, provide some diversity in structural configuration (e.g., some invertebrate taxa such as beetles take cover under woody debris, and covers serve as attractants for such species), and reduce the frequency of vertebrate (non-target taxa) captures (Lemieux and Lindgren 1999). I covered half the pitfall traps with flat woody material or rocks suspended between 0.5 to 1.5 cm above the trap, while the other half the traps were left uncovered. Observers took care to ensure that material or animals were not attached to the covers. These configurations are equivalent to, or more intensive than, those used

in most studies of invertebrates (e.g., Kharboutli and Mack 1993, Crist and Wiens 1995, Oliver and Beattie 1996a, Duelli and Obrist 1998, Matthiessen and Learmonth 1998, Simmons et al. 1998).

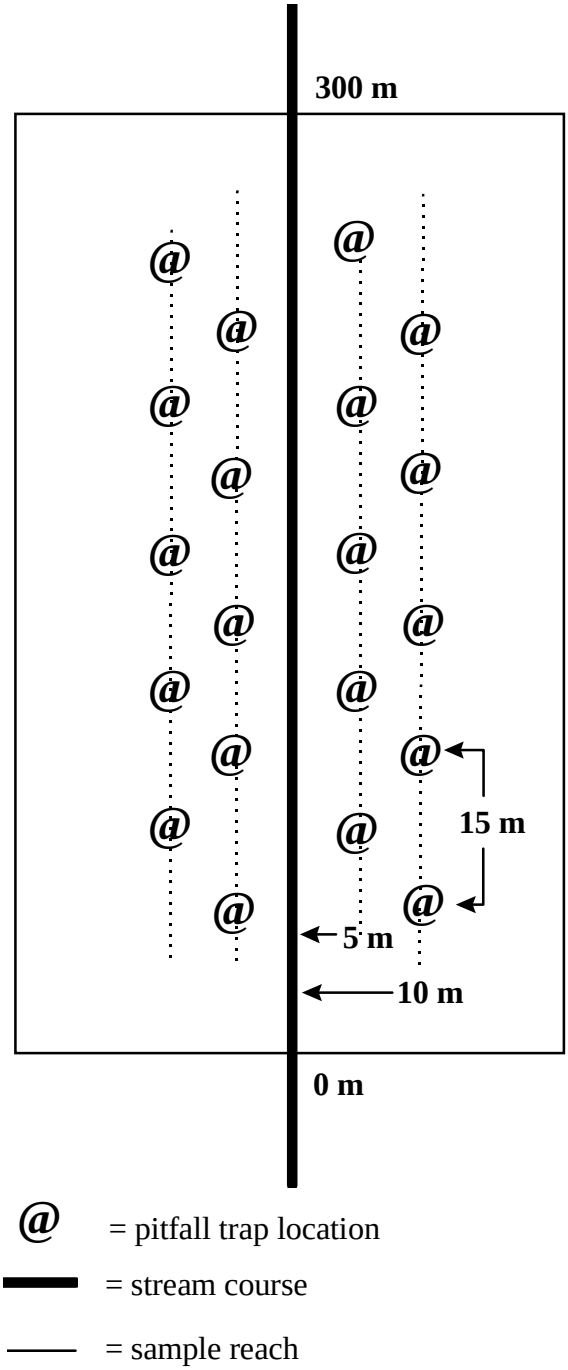

FIG. 10. Location of pitfall traps on each sample reach to sample invertebrates in the Lake Tahoe basin.

Observers opened traps by 1600 hrs on day 1, left them open for 2 nights, and removed them in the afternoon of day 3 for an approximately 48-hour trapping period, and a total of 960 trapping hours per reach and 3200 trap nights across all reaches. Trapping periods vary widely among studies, ranging from multiple days (e.g., Gotelli 1996, Pavuk et al. 1997) to multiple weeks (e.g., Oliver and Beattie 1996a, Holway 1998, Matthiessen and Learmonth 1998), however 3 to 4 days is common (e.g., Crist and Wiens 1995, Gotellie 1996, Pavuk et al. 1997). The trapping period combined with the number of traps used in this study is commensurate with approaches used and demonstrated to be effective in other studies employing these shorter trapping periods. Shorter trapping periods are likely to miss less common species and may have missed less common families, but the primary objective of sampling was to assess the relative richness of various sites. I conducted trapping once on each reach between June 3 and August 22 in 1995 and 1996, with a median sampling date of June 12. Sampling occurred during the same general period between years (Fig. 11), with the majority of sampling (99%) occurring in June and July. The latest dates were associated with the highest elevation reach sampled, and it was sampled in 1995 which was a longer winter with higher precipitation than the winter of 1996. I staggered sampling by elevation in an attempt to sample at a similar phenological stage across reaches for each visit.

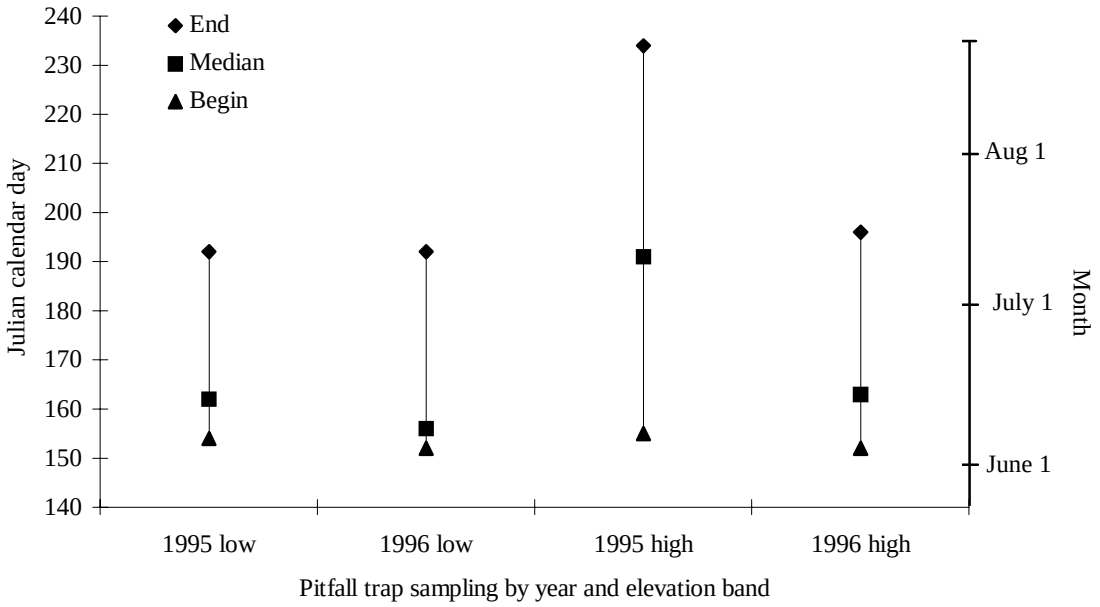

FIG. 11. Pitfall trap sampling periods by year and elevation band. Sample reaches were divided into 2 elevation bands: low (< 2100 m) and high (≥ 2100 m). Data were collected in the Lake Tahoe basin, 1995 to 1996.

To facilitate analysis of inter- and intra-year variation in captures, I conducted a second round of trapping in 1995 in addition to resampling 8 reaches in 1996. This second visit in 1995 was conducted at least 4 weeks after the first visit, and occurred in July or August (Table 5). These data were used as a context for interpreting inter-year variation.

TABLE 5. Pitfall trap sampling dates in 1995 and 1996 on 8 sample reaches in the Lake Tahoe basin.

Reach	1995 Visit 1	1995 Visit 2	1996 Visit
Burton 4	June 28	July 22	June 27
Griff 4	June 5	July 1	June 5
McFaul 3	-	July 18	June 4
Meeks 4	July 10	August 30	July 25
Saxon 4	June 7	July 18	June 5
Slaughterhouse 1	June 12	July 11	June 4
Third 4	August 22	September 6	July 22
Ward 2	June 28	August 1	June 10

Animals captured in the pitfall traps were processed in the following steps. First, I emptied the composite sample of pitfall trap contents from a reach onto a fiberglass screen laid over a cotton cloth suspended over a plastic sorting tray (40 cm long, 30 cm wide, 13 cm deep). Larger material was captured by the screen, and smaller material captured by the cotton cloth. Small mammals (primarily *Peromyscus* and *Sorex*) were also captured in the pitfall traps. Observers removed all mammals from the sample at this point in the process. Observers washed invertebrates off the screen into a pan with water and picked through the contents for 20 person-min to remove all unique-looking individuals. Smaller animals captured by the cotton cloth were scraped off the cotton cloth. I stored each sample of invertebrates in a plastic bottle containing 70% ethyl alcohol for later identification. A total of 3 observers keyed invertebrates to family (whenever possible), 2 of whom keyed animals in both years. Mammals were keyed to species, labeled, and preserved by freezing.

Riparian Searches

Riparian searches consisted of 3 components: walking surveys, intensive-search plots, and channel searches (Fig. 12). The riparian search was a less taxa-specific sampling technique intended to detected a broader array of taxa than the more taxa-specific sampling techniques were designed to detect. Its strength is the ability to survey a large area in a relatively short period of time and describe the breadth of taxa that occur there. Data collected by riparian searches complement data collected by more intensive, taxa-specific techniques (bird, small mammal, plant, and invertebrate sampling). Riparian searches were the only source of data on fungi richness and composition.

Walking Surveys

Walking surveys consisted of a time- and area-constrained search, where observers searched within 30 m of bankfull channel on each side of the channel for the full 300 m length of the sample reach (Fig. 12). One observer was located on each side of the channel and searched at a pace of 30 min per 100 m for a total of 180 search-min per reach. Observers walked downstream, searching by meandering within the reach area and visiting the channel and outer extent of the reach at least twice per 100 m. Walking surveys were intended to detect species in the terrestrial portion of the sample reach. They were conducted in the downstream direction to position observers to search the channel in the upstream direction (see next section) and minimize disturbance from observers within the reach.

Observers searched by listening, visually scanning the area, and physically searching (e.g., looking under rocks and logs, raking duff) for individuals or sign of focal species. Observers spent an approximately equivalent amount of time searching the ground, understory and overstory levels. Observers were equipped with a hand rake, binoculars, and hand lens. Search time was

strictly monitored. Observers suspended search time if data recording required more than 30 seconds.

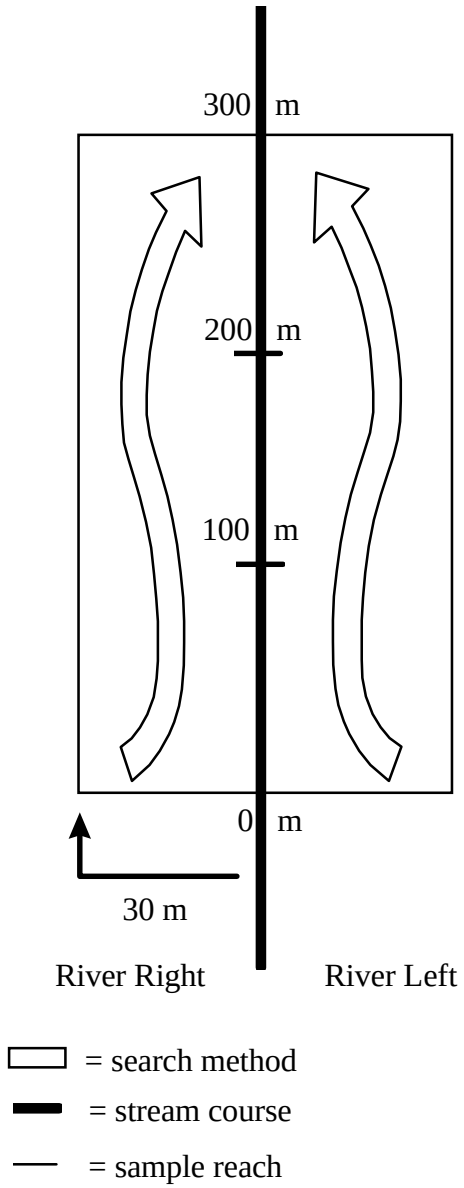

FIG. 12. Configuration of riparian searches on each reach sampled in the Lake Tahoe basin.

Walking surveys recorded only a subset of all taxa potentially encountered. No survey technique or amount of effort can guarantee that all species will be detected, particularly rapid assessment methods. As such, walking surveys recorded all vertebrate detections and all macrofungi genera within the sample reach, plus any target or "focal" species. Focal species of invertebrates and vascular plants met one or more of the following criteria: 1) they are visually or audibly detectable during a slow-paced walking survey; and 2) they are riparian obligates or have specific riparian habitat requirements. As such, focal species had a high probability of detection using the walking survey method. Although the sample reaches encompassed a wide range of vegetation types that may have differential effects on species detectability, the sample reaches were relatively narrow and it was not difficult to detect species even in the most dense vegetation.

Intensive-search plots

I established a randomly-located, intensive-search plot within each 100-m segment (at 50 m, 150 m, and 250 m) of the reach, for a total of 6 plots, to more comprehensively survey composition. The intensive-search plot was a 5 x 10-m plot whose length was located perpendicular to the channel, and whose extent was determined by pacing the dimensions. In the first 100-m segment of a reach (0 to 100 m), the distance of the plot from bankfull channel (0 m, 10 m, or 20 m) was randomly selected. Intensive-search plots in the 2 remaining 100-m segments (100 to 200 m and 200 to 300 m) were sequentially placed in the other 2 locations (e.g., if the first location chosen was 20 to 30 m, the next 2 plots were placed at 0 to 10 m and 10 to 20 m, respectively). Observers located plots in the field by pacing the distance from the channel and marking the boundary of the plot by locating field markers (e.g., visually obvious items at the approximate corners of the plot) or temporarily flagging the perimeter of the plot.

Observers collected the following data in intensive-search plots: a 10-min point count for birds, a list of all vascular plant species and genera of macrofungi, and a 10-min search for all terrestrial vertebrates and invertebrates. The protocols conducted within the intensive-search plots follow standard protocols for sampling birds (Ralph et al. 1995), reptiles and amphibians (Corn and Bury 1990, Heyer et al. 1994), and plants (James and Shugart 1970, Mueller-Dombois and Ellenburg 1974).

Channel Searches

Channel searches were the aquatic equivalent of riparian searches, and in this study, constituted the only sampling conducted in the channel. Channel searches consisted of walking up the stream reach in and along the margin of the wetted stream channel (Fig. 12). In streams 2 m wide or less, only 1 observer was required to conduct the channel search; in larger streams, 2 observers conducted the search. Observers conducted channel searches between 1000 and 1700 hrs. The same observers were involved in conducting both the riparian and channel searches at a given reach.

Data collected during the channel search were similar to data collected during riparian searches, with the exception of a few water descriptors. Observers walked at a pace of 15 min per 50 m, searching for and recording all focal species (see walking survey for specific taxa) detected. If alone, the observer alternately meandered across the channel, surveying each side of channel equivalently. If 2 observers conducted the search, they walked parallel in the channel surveying their half of the channel, with both observers surveying the middle of the channel. When 2 observers surveyed a channel, one recorded the observations of both observers to avoid duplicate detections. At the 25 m, 50 m and 75 m mark within each 100 m segment, an intensive in-channel search was made for 1 m across the entire width of the channel, termed a belt transect. Belt transects were not strictly timed, but observers searched and recorded information for approximately 5 person-minutes per meter of channel width.

Riparian Search Sampling Schedule

Riparian searches were conducted between 0530 and 0930 hrs. Reaches were sampled once, with 32 reaches sampled in 1995, and 48 in 1996. Sample dates were closely timed between years to minimize variation in phenology between years. For the purposes of display, sample dates were grouped by low (< 2100 m) and high (≥ 2100 m) elevation, and show that median sample dates were within 4 days between years within each elevation band (Fig. 13).

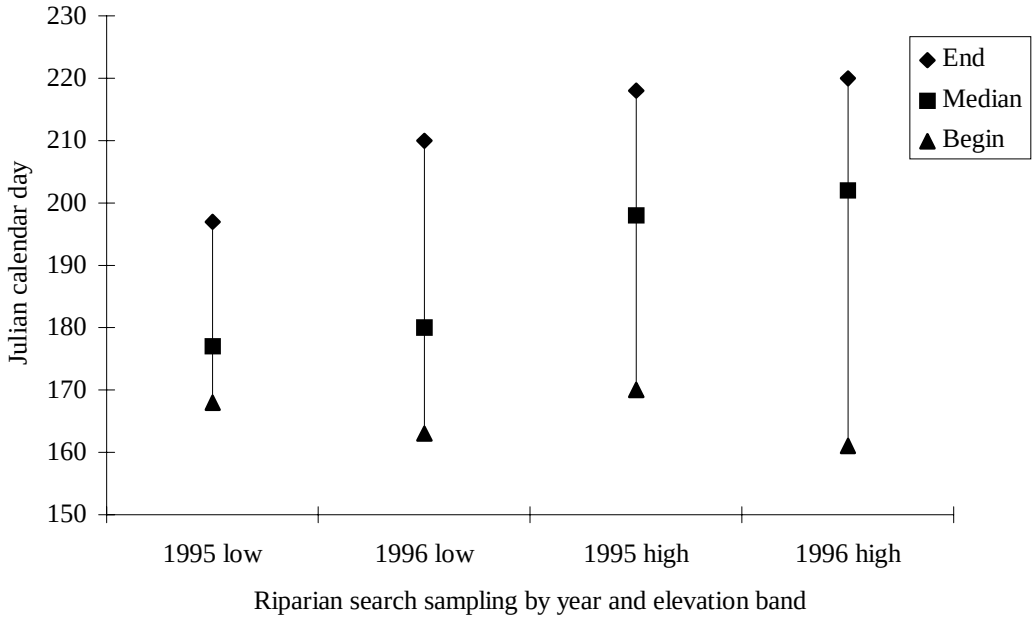

FIG. 13. Sample dates for riparian and channel searches by year and elevation band. Sample reaches were divided into 2 elevation bands: low (< 2100 m) and high (≥ 2100 m). Data were collected in the Lake Tahoe basin, 1995 to 1996.

Fifteen observers participated in riparian and channel searches, 3 of whom collected data in both years (Appendix 4). Observers trained together for 4 weeks before data collection began. Two observers collected data at each reach, and observer pairs were mixed among reaches to minimize any potential for observer bias in reach comparisons.

To facilitate analysis of inter- and intra-year variation in captures, I conducted a second round of riparian search and sweep-net sampling in 1995, in addition to resampling in 1996 (Table 6). The first visit in 1995 and 1996 was conducted in June or July, and sampling was staggered by elevation in an attempt to be sampling at similar phenological stage across reaches. The second visit in 1995 was conducted at least 4 weeks after the first visit, and occurred in July or August. The 1995 visit closest to the 1996 sample date was chosen for inter-year comparisons. If 1995 dates were equidistant from the 1996 visit date, the latter date in 1995 was chosen because 1995 was a longer winter (i.e., later spring) compared to 1996. In relation to the resample reaches, a total of 13 observers collected sweepnet data, with 3 observers common to both years (Appendix 4). Three observers keyed the specimens to the family level, with 2 observers common to both years.

TABLE 6. Sample dates for sweepnet and riparian search sampling conducted at sample reaches in the Lake Tahoe basin. Bolded dates in 1995 are those closest to sample dates in 1996 for the corresponding reach, and indicate the 1995 visit used in inter-year comparisons.

Reach	1995 Visit 1	1995 Visit 2	1996 Visit
Burton 4	June 27	**August 9**	July 31
Griff 4	**June 27**	August 9	June 20
McFaul 3	**June 27**	August 16	June 20
Meeks 4	**July 20**	September 6	August 6
Saxon 4	**June 20**	August 3	June 18
Slaughterhouse 1	**July 7**	August 15	June 13
Third 4	July 7	**August 24**	August 6
Ward 2	July 13	**August 29**	August 13

Sweepnet Sampling

Aerial and vegetation-associated invertebrates were sampled by sweep netting vegetation at 6 locations along each reach (Fig. 12). Sweepnets consisted of 38-cm diameter cotton nets mounted at the end of 1.5-m long aluminum poles. Sweep netting is one of the most widely used techniques in insect population sampling from vegetation (Southwood 1978, Pedigo 1996). Its advantages are its simplicity and speed; its disadvantages are it is biased toward capturing individuals that do not fall off or fly away on the approach of the collector (Southwood 1978).

Sampling was conducted within a 20-m radius of center of the 6 intensive-search plots established for riparian searches (see previous section). A total of 30 sweeps were taken at each plot, 10 sweeps at each of 3 height classes: low (<1m, grasses/herbs), medium (1 to 2m, willows/alders/shrubs), and high (>2 m, trees). The number of sweeps necessary to obtain a mean abundance that is within 25% of the true value has been investigated by a number of authors, and estimates range from 10 to 25 sample units, each sampled by 25 sweeps (Gray and Treloar 1933). The sweepnet data collected here was only used, along with other invertebrate data sets, to describe composition. As such, the sampling intensity conducted for each reach (6 units each sampled by 30 sweeps) appeared adequate to describe composition.

Collectors could effectively sample vegetation up to approximately 3.5m high and all specimens captured were collected. As wide a variety of vegetation was swept as possible. Sweeps were made by aggressively moving through the vegetation with the net. Sweepnet samples were taken in the late morning or early afternoon on the same day as the riparian searches. Sampling was not conducted if it was precipitating or if the wind was greater than a slight breeze. All animals collected were emptied into a killing jar (ethyl acetate) or a vial containing 70% ethyl alcohol for preservation and identification.

Plant Walks

Plant species composition was described in greater detail using a walking survey method. The survey consisted of a 60 and 180-min search, noting the presence of individual plant species. In 1995, 8 reaches (one in each watershed) were searched for 180 minutes each. Observers attempted to encounter and record as many plant species as possible within the time allotted. In 1996, all 56 reaches sampled that year were searched for 60 minutes each. This time, the observers were supplied with a plant list from the riparian channel search. Observers attempted to encountered and record as many new plant species as possible within the time allotted. In both 1995 and 1996, two individuals conducted all the plant searches, and each year both individuals had extensive knowledge of the flora and trained together for several days before conducting separate searches (Appendix 4). Each search was constrained to the length and width of the reach, but the observer was free to meander unconstrained within the time and space limits

applied. This allowed the observer to spend more time in complex habitats and less time in simple habitats. All plant species detected were recorded. If the identification of a plant was not known, the specimen was collected and keyed at the lab. Time spent collecting specimens was not counted against the search time.

DATA ANALYSIS

In general, α (alpha) levels of ≤ 0.10 were used to identify significant results; exceptions to this practice are noted in association with specific analyses. An α of 0.10 was used, as opposed to the standard α level of ≤ 0.05 (Sokal and Rohlf 1981:164), because I was looking to establish patterns of association versus testing hypotheses. The higher α level increases the risk of considering conditions as different or relationships as existing, when they may not be so (Type I error), but concomitantly it decreases the risk of considering conditions as not differing or relationships as not existing when they truly do (Type II error) (Sokal and Rohlf 1981:159).

Environmental Variables

Environmental sampling resulted in 3 variable sets: abiotic environment, channel characteristics, and vegetation characteristics. A discussion of the variables in each set is provided below.

Abiotic Environmental Variables

Four variables were used to describe the abiotic environment: elevation, precipitation, reach aspect, and basin orientation (Table 7). Aspect of reaches was described by categorizing aspect into 1 of 4 cardinal directions: north (316-45°), east (46-135°), south (136-225°), and west (226-315°) based on the average of 30 aspect readings along the channel. Four basin orientations were established (south side, west side, north side, and east side), and watersheds (and their reaches) were assigned to an orientation. Aspect and orientation are typically analyzed as categorical variables because central tendency has no ecological meaning.

Channel Variables

Three channel variables were created to characterize channel morphology: gradient, sinuosity, and width (Table 7). Channel gradient was calculated as the average of the 3 measures of percent slope taken with a clinometer. Channel width was calculated as the average of the 30 width measurements taken along the reach. Sinuosity was calculated at the ratio of the length of the channel and the straight-line distance between the beginning and end of the reach (Gordon et al. 1992, Allan 1995).

TABLE 7. Environmental variables for lotic ecosystems used in analysis, including their metrics and the transformations used in principal components analysis and regressions. Dashes indicate no transformations were used.

Environmental Variables	Metric	Transformations for PCA and Regression Analyses
Abiotic environment:		
Average elevation	M	ln(x+1)
Average annual precipitation	Cm	ln(x+1)
Reach aspect	N, E, S, W	-
Basin orientation	north, east, south, or west side	-
Channel characteristics:		
Average channel gradient	%	ln (x+1)
Average channel width	M	ln (x+1)
Channel sinuosity	length/distance	ln (x+1)
Vegetation characteristics:		
Mixed conifer	proportion of reach	arcsine $\sqrt{x}$
Lodgepole pine	proportion of reach	arcsine $\sqrt{x}$
Subalpine conifer	proportion of reach	arcsine $\sqrt{x}$
Aspen/cottonwood	proportion of reach	arcsine $\sqrt{x}$
Alder/willow	proportion of reach	arcsine $\sqrt{x}$
Shrub	proportion of reach	arcsine $\sqrt{x}$
Meadow	proportion of reach	arcsine $\sqrt{x}$
Canopy cover index	proportion covered	-
Small snags (10-50 cm dbh)	snags/ha	ln(x+1)
Large snags (>50 cm dbh)	snags/ha	ln(x+1)
Small logs (25-50 cm diameter)	m/ha	ln(x+1)
Large logs (>50 cm diameter)	m/ha	ln(x+1)
Channel log volume	m^3/ha	-

Vegetation Variables

The large number of CNPS vegetation types and habitats encountered (n = 25) relative to the number of sample reaches precipitated the need to group vegetation types into vegetation classes. Seven vegetation classes were created: meadow, mixed conifer, subalpine conifer, lodgepole pine, shrub, aspen−cottonwood, and alder−willow. All but the lodgepole pine vegetation class represented more than one CNPS vegetation type (Appendix 5). Multiple CNPS vegetation types were combined into single vegetation classes based on a variety of criteria including frequency of occurrence, similarity in species composition, moisture regime associations, co-occurrence in the field, ability to distinguish in the field, and physiognomic structure. For example, the alder−willow group was formed by combining the alder series and montane wetland shrub (predominantly willow) habitat as defined by Sawyer and Keeler-Wolf (1995). These 2 types were intermingled throughout the study area, were often difficult to separate at a given site, and are similar in form and function. Similarly, the aspen−cottonwood group was formed by

combining the aspen and black cottonwood series because these series occur in similar soil moisture regimes, have similar physiognomy, and co-occurred on many reaches.

Vegetation structure was described by 7 variables: canopy cover index, small and large log density, small and large snag density, and channel log volume (Table 7). Canopy cover index was reported as a percent. Logs were calculated as the number of meters of logs per hectare in each of 2 diameter classes (small = 12 to 50 cm diameter; large = > 50 cm diameter). Snags were reported as the total number of snags per hectare in each of 2 dbh classes (small = $\geq$ 25 cm to 50 cm dbh; large = > 50 cm dbh). Channel log volume was reported as cubic meters of logs per hectare of channel area.

Disturbance Variable

One meso-scale variable was derived to represent disturbance in the vicinity of the reach. The meso-scale disturbance variable, neighborhood disturbance, was calculated as the proportion of the area within 250 m of the reach that was disturbed. Neighborhood disturbance was used to represent disturbance when disturbance was a potential covariate.

Biodiversity Measures

Overview of Measures

The basic measures of diversity were calculated similarly for each taxonomic group. Biological diversity was described by richness, frequency of occurrence, and abundance (measures of alpha diversity), changes in species composition along environmental gradients (beta diversity), and rarity (Table 8). Only native species were included in the analysis. The richness and composition of exotic species can provide insights into threats to biological diversity, but such an analysis was beyond the scope of this study.

TABLE 8. Biological diversity measures used to describe three facets of biological diversity in the Lake Tahoe basin.

Biological diversity measure	Alpha diversity	Rarity	Beta diversity
Richness	X	X	
Abundance	X		
Composition			X

Alpha Diversity Measures

The most common metrics of alpha diversity are species richness and abundance. Species richness is a direct measure of a popular aspect of biological diversity (Noss 1990), and is used widely for conservation planning (e.g., Thomas and Mallorie 1985, Williams et al. 1996). In this study, alpha diversity was based on richness for all taxa, and was additionally represented by relative abundance for birds and mammals (Table 8). Richness was calculated for given taxonomic groups, as well as for taxa associated with aquatic, riparian, and upland environments within some taxonomic groups (vertebrates and vascular plants)., Mathematical indices of biological diversity are commonly used to quantify diversity (Pielou 1975, Magurran 1988), however they each have different sensitivities and biases, and can be difficult to interpret (Magurran 1988). As a measure of diversity, species richness complies with many suggested criteria for a strong measure: non-parametric and statistically accurate, applicable to any community independent of species abundance distribution, small bias and sampling variance in samples of moderate size, and strict concavity meaning that the total diversity in a pooled set of communities equals or exceeds the average diversity within communities (Lewontin 1972, Lande

1996). Species richness complies with all of these criteria, and was used as the measure of alpha diversity in my study.

Rarity Measures

Unless analyzed as a separate group, the associations of rare species are commonly masked by, (1) the presence of common species in every richness calculation, and (2) non-significant, species-specific relationships resulting from small sample size. Rarity was identified based on frequency of occurrence of taxa within each taxonomic group, one of 3 common approaches to identifying rarity (Fisher et al. 1943, Kempton 1979, Gaston 1994). I consistently defined rare taxa for all taxonomic groups as those occurring on < 10% of sample reaches. By defining rarity relative to other species in the study area, I addressed taxa with intrinsic rarity (based on evolutionary history, spatial distribution, and genetic structure [Stebbins 1980]), induced rarity (resulting from human influences), and pseudo-rarity (resulting from detection probability [Gaston 1994]). The use of a consistent rule set by which to define rarity facilitated the comparison of environmental relationships of rare and common taxa across taxonomic groups.

Detection probability, although variable among taxa, is relatively consistent among species or taxa within a taxonomic group and among sample reaches. Therefore, detection probability is assumed to be a negligible contribution to the observed composition of rare species within each taxonomic group. In addition, the focus of the analysis on relative changes in the number of rare species per taxonomic group minimizes the potential bias to observed patterns of rarity introduced by differences in detection probability.

Beta Diversity Measures

Turnover in species composition across a gradient is the crux of beta diversity. Beta diversity was based on changes in the occurrence of taxa across environmental gradients. I chose to use 3 measures to describe beta diversity and rank gradients. As the primary measure of beta diversity I calculated the absolute number of taxa turning over along a gradient. Specifically, this means the number of taxa gained and lost as one moves from one portion of a gradient to another. I used the lowest of these 2 values (gains or losses) to represent the turnover of taxa ("total turnover"). In addition, I looked at which taxa were being lost or gained between 2 portions of a gradient, and identified only those taxa occurring on more than one sample reach (i.e., those with the potential to occur in both portions of the gradient being analyzed). This taxa count ("core turnover") was complementary to total turnover, and assisted in the interpretation of the relative contribution of gradients to beta diversity.

I used a modified version of Whittaker's index (β_w; Whittaker 1972) as a secondary measure of beta diversity. Whittaker's index is considered one of the best measures of beta diversity based on the ability to reflect degree of community turnover, exhibiting properties of additivity along gradients, independence from alpha diversity, and independence from sample size (Wilson and Shmida 1984, Magurran 1988). β_w is calculated as the total number of species occupying 2 sites divided by the average number of species at each site. However, Harrison et al. (1992) proposed a modified version of Whittaker's index that increases its independence from alpha diversity without sacrificing its performance relative to the other 3 criteria. The modification entails changing the denominator of the equation from the average number of species to the lowest number of species at either site. Since the difference between the lower number and higher number is essentially alpha diversity, this modified index reports a sort of minimum beta diversity. I used this modified version of Whittaker's beta diversity index (β_{wMIN}) in this study:

$$\beta_{wMIN} = (S/s\text{-}max)\text{-}1,$$

where S = total species richness, and s-max = the highest of the two richness values being compared.

Absolute counts of turnover and β_{wMIN} provide different perspectives on beta diversity. Absolute counts of taxonomic turnover, much like species richness, serve as direct measures of beta diversity. Whittaker's index is a relative measure of species turnover in that the index value reflects the relative magnitude of absolute turnover to the total number of taxa occurring across portions of the gradient being analyzed. Absolute measures of turnover facilitate the calculation of absolute turnover across taxonomic groups, a feature of value in this study. Alternatively, the relative nature of Whittaker's index provides a view of the ecological significance of one or more gradients to the beta diversity of a taxa. For more speciose taxonomic groups (e.g., invertebrates), the turnover of one species may not be as ecologically significant as it would be for a less speciose group (e.g., vertebrates). Consequently, these 2 measures provide different and yet complementary information on beta diversity and its contribution to gamma diversity.

Vertebrate Diversity

Vertebrates were analyzed by class: birds (Aves) and mammals (Mammalia). Bird and mammal detections from each sampling method were described by simple summary statistics. Abundance data were only available for birds and mammals, and only one method provided abundance data for each class. Presence data were provided by multiple data sets per vertebrate class, and variables describing taxonomic richness were derived by combining data in that class from all sample methods. For each class of vertebrates, descriptors of alpha diversity, rarity, and beta diversity were derived and analyzed (Table 9). The primary analysis unit for birds, mammals and plants was species, whereas invertebrates were analyzed at the family level, and fungi were analyzed at the genus level.

TABLE 9. Biological variables used to describe sample reaches in the analysis of biological diversity of the Lake Tahoe basin. B = birds, M = mammals, I = invertebrates, P = vascular plants, and F = fungi.

		Taxonomic group				
Variable	Metric	B	M	I	P	F
Taxonomic richness	sum of unique taxa	X	X	X	X	X
Total abundance	average number of individuals	X	X			
Frequency of occurrence	number of reaches with presence	X	X	X	X	X
Taxa abundance	average number of individuals	X	X			
Richness by habitat	sum of species	X	X	X	X	
Richness by freq. class	sum of species	X	X	X	X	X
Abundance by family	sum of individuals per family	X				

Birds

Birds were routinely identified to species. However, some observations were recorded above species level (e.g., hummingbird, woodpecker drumming). All unique observations per reach were used for calculations of richness and total abundance, but observations above the species level were excluded from all other analyses (i.e., richness by habitat association or rarity, and beta diversity). Observations above the species level comprised < 1% of all observations, and included one genus (*Accipiter*), 5 families (Sphycadae, Trochilidae, Hirundinidae, Picidae, and Fringillidae), and 2 bi-species groups (*Picoides* and *Empidonax* sub-groups). A Picoides sub-group (white-headed woodpecker, *Picoides albolarvatus*, and hairy woodpecker, *P. villosus*) was used in species richness calculations because in 54% of the observations (n = 84) observers were

unable to distinguish the most common call of these 2 species. Two additional *Picoides* species were observed in the study area and treated separately (*P. arcticus and P. pubescens*). Similarly, an Empidonax sub-group (dusky flycatcher, *Empidonax oberholseri*, and Hammond's flycatcher, *E. hammondii*) was used in species richness calculations because in 26% of the observations observers were unable to distinguish these 2 species. Two other *Empidonax* species were detected in the study area and treated separately (*E. trailii*, and *E. difficilus*). The need to combine these species into sub-groups is fairly common (e.g., Hejl et al. 1988). Only observations at the species level were used in compositional analyses (i.e., beta diversity)

Frequency and abundance estimates were calculated for each species, and they were derived from different data sets. Frequency of occurrence estimates were derived from a combination of point count and riparian survey data. Abundance estimates for each species were calculated by averaging the number of individuals detected per point count across all 3 visits.

Patterns of alpha diversity in birds were further examined by looking at diversity by habitat association (Appendix 7). Species were categorized based on published data on life history characteristics and habitat relationships (e.g., Ehrlich et al. 1988, Zeiner et al. 1990a) into one of 3 habitat-association groups: aqua-dependents (n = 11 species), riparian-meadow–associates (n = 28 species), and upland associates (n = 61 species).

Bird species were categorized into one of 2 frequency classes: rare (< 10% frequency), and common ($\geq$ 10% frequency). The number of species ascribed to each frequency class were similar, with 49 species considered rare and 52 species considered common (Appendix 7).

Mammals

Mammals were routinely identified to species. However, a few observations were recorded above the species level. All unique observations per reach were used for calculations of total richness and total abundance. Observations above the species level comprised approximately 2% of all observations, and included 3 genera (*Mustela, Sorex, and Lepus*). All genera observations were included in calculations of taxonomic richness where they were not already represented at the species level. In calculations of species richness, weasel (*Mustela*) and shrew (*Sorex*) observations were pooled at the genus level, and included in calculations of richness, along with *Lepus* sp. observations. Only observations at the species level (with the exception of *Lepus* sp.) were used in compositional analyses (i.e., beta diversity).

Frequency and abundance estimates were derived from different data sets. Frequency of occurrence estimates were derived from 4 data sources: Sherman trap, riparian search, pitfall trap, and point counts (Douglas squirrel only). Although mammals were not the target taxa for point counts and pitfall trapping, these methods provided a substantial and representative sample for Douglas squirrels and shrews, respectively. Point counting has been shown to provide a good relative index to Douglas squirrel abundance, and in this study, may provide the best index of Douglas squirrel abundance across reaches. Douglas squirrels are one of the largest bodied species captured in the Sherman traps, and it is likely I did not capture a representative sample of the population. Riparian searches provided the only data on medium and large-bodied mammals, such as deer, bear, and coyote. Most detections were based on sign (e.g., tracks, scat), but some were direct observations of individuals. Abundance estimates were available for small mammals only, being derived from Sherman trap data only (the only source of abundance data). The number of first captures was divided by the number of trap nights to derive a catch-per-unit-effort, relative abundance measure (Kelt et al. 1994, Schweiger et al. 1999).

Patterns of mammal alpha diversity were further explored by looking at diversity by habitat association (Appendix 8). Mammal species were categorized into one of 2 habitat-association groups based on published data on life history characteristics and habitat relationships (Zeiner et al. 1990b, Hall 1995): aquatic–riparian–meadow associates (n = 12 taxa), and upland associates (n = 23 taxa).

Mammal species were also categorized into one of 2 frequency classes: rare (occurring on < 10% of the reaches) and common (occurring on ≥ 10% of the reaches). Seventeen species were classified as rare, and 18 species were classified as common.

Invertebrate Diversity

Invertebrates were routinely identified to family. Observations above the family level were included in calculations of taxonomic richness, but were excluded from all other analyses (i.e., richness by habitat association or rarity, and beta diversity). Assessing alpha diversity at the family level has been demonstrated to closely reflect diversity at lower taxonomic levels (Williams and Gaston 1993), and a number of studies have successfully detected relationships between diversity and environmental conditions by characterizing invertebrate diversity at the family level (e.g., Smith et al. 1990, Feldman and Connor 1992, Ormerod et al. 1994, Gardner et al. 1995, Butler et al. 1997).

All specimens in the Lepidoptera family were identified to genus. Butterflies have been suggested as good indicators of biological diversity for many reasons, primarily because they occupy a variety of ecological niches and they are relatively easy to sample and identify to species (Daily and Ehrlich 1995). I analyzed patterns of richness of Lepidoptera genera.

Invertebrate richness and composition for each reach were determined based on a combination of sweepnet, pitfall trap, and riparian search sampling. Inter-year differences in composition and richness (see Chapter 3) restricted diversity analyses to 1996 data because it had the largest sample size (n = 56 reaches). Although I only analyzed one year's data, others have obtained consistent results from year to year in relative comparisons of diversity among sites (Daily and Ehrlich 1995).

Invertebrate families were categorized based on published data on life history characteristics and habitat relationships (Borror et al. 1989) into one of 3 life-history traits: aquatic, semi-aquatic, and terrestrial (Appendix 9). Aquatic invertebrates included families that spent all or the majority of their life span in an aquatic environment. Semi-aquatic invertebrates included families that typically live in damp marginal habitats, or had an aquatic larval or pupal stage that did not dominate their life span (Ward 1992). A total of 28 families were classified as aquatic, 12 as semi-aquatic, and 163 as terrestrial.

Invertebrate families were also categorized into one of 2 frequency classes: rare (occurring on < 10% of the reaches) and common (occurring on ≥ 10% of the reaches) (Appendix 9). A total of 108 families were classified as rare, and 97 families were classified as common.

Vascular Plant Diversity

Plants were routinely identified to species; observations at higher taxonomic levels were rare and were excluded from all analyses. Plant species richness and frequency of occurrence were derived from 2 sources: plant walk and riparian search data.

Patterns of plant alpha diversity were further explored by looking at diversity by habitat association Plant species were categorized based on published data on life history characteristics (Hickman 1993, Dennis 1995) into one of 2 habitat-association groups: aquatic–riparian–meadow associates (n = 213 species), and upland associates (n = 257 species) (Appendix 10).

Plant species were also categorized into one of 2 frequency classes: rare (occurring on < 10% of the reaches) and common (occurring on ≥ 10% of the reaches). The number of plant species in each frequency class was not equivalent, with 290 species classified as rare, and 180 species classified as common (Appendix 10).

Fungi Diversity

Fungi specimens, including both fleshy fungi and lichen, were routinely identified to genus. Fungi genera richness and frequency of occurrence were derived from riparian search data. Observations at higher taxonomic levels were rare and were excluded from all analyses. Fleshy

fungi and lichen genera were treated separately in basic analyses of environmental relationships. In all other analyses (i.e., beta diversity and rarity), all fungi genera were analyzed together.

Fungi genera were categorized into one of 2 frequency classes: rare (occurring on < 10% of the reaches) and common (occurring on $\geq$ 10% of the reaches) (Appendix 11). The number of fungi genera in each frequency class was not equivalent, with 43 genera classified as rare, and 12 genera classified as common (Appendix 11).

Statistical Analysis

Environmental Conditions

Environmental variables (Table 7) were used to describe the environment and as explanatory variables for patterns of diversity. Environmental variables were first summarized using descriptive statistics (i.e., average, standard error, range). Principal components analysis (PCA) was used to identify gradients of variation in environmental conditions. Environmental variables were partitioned into 3 groups: physical features (a combination of abiotic and channel variables), live vegetation structure and composition (vegetation types and canopy cover), and woody debris (snag and log variables). Variables were transformed if needed to better approximate a normal distribution (Table 7) and then standardized by subtracting the mean and dividing by the standard deviation so they had an equivalent magnitude (Sokal and Rohlf 1981, Jongman et al. 1995:130). An equamax rotation was used to improve the ability to interpret the factors (SPSS 1993:65). Equamax rotation is a combined attempt to minimize the number of variables associated with each factor and the number of factors needed to explain the variation. All eigenvalues $\geq$ 1.0 were reported and discussed. Eigenvalues of less than 1.0 explain no more variance than a single variable, and do not contribute to the objective of identifying major gradients of variation (SPSS 1993:54). Factor scores from the physical and vegetation principal components were compared using Pearson's correlations and linear regression to determine relationships among them. Finally, variation in environmental characteristics and gradients by basin orientation was described using analysis of variance (ANOVA) (Sokal and Rohlf 1981, Hair et al. 1992). The specific application of these statistical techniques is described in more detail below in the assessment of alpha diversity, rarity, and beta diversity.

Individual environmental variables and factor scores associated with each environmental gradient were used as explanatory variables in the analysis of taxonomic richness. This approach has been used successfully in other studies to explore the interrelationships of measures of richness or diversity with major environmental gradients (e.g., Anderson et al. 1983, Owen 1990, Kelt et al. 1994). Pearson's correlation coefficient and linear regression were used widely to describe relationships between diversity measures and environmental characteristics. Specific applications of these techniques are described below. In all applications, correlation and regression coefficients were consistently interpreted in the following manner: $r < 0.20$ was considered a weak relationship; $0.20 \leq r < 0.40$ was considered a moderately strong relationship; $r \geq 0.40$ was considered a robust relationship.

Patterns of Alpha Diversity

Patterns of alpha diversity represented by various measures (i.e., richness and abundance across all species and for species groups based on habitat association) and their relationships with environmental conditions were first explored by looking at bivariate scatter diagrams and linear correlations (Campbell 1989, Ellison 1993). The scatter diagrams and linear correlations provided information on existence and linearity of relationships. Pearson's correlation coefficient was used to identify correlations between variables.

Principal components analysis (PCA) was used to identify gradients in the abundances of birds and mammals. Gradient analysis identified patterns of distribution and abundance of taxa among sample reaches. The gradient analysis for mammals was performed on small mammal

species (and 2 genera, *Mustela* and *Sorex*) detected during small mammal trapping. The gradient analysis for birds was restricted to bird family abundance because the number of species was too great relative to the number of sample reaches. Average family abundance was calculated based on the average number of detections per point count per reach. A frequency of 10% was used as a limit for inclusion of taxa into the bird and mammal analyses to ensure the PCA reflected major gradients in composition across reaches. Log-normal transformed variables were used for each analysis.

Multiple linear regression was used to identify environmental variables (independent variables) that best predicted the values of a biological diversity variable (dependent variable). Step-wise multiple regressions were used to describe relationships between the richness and abundance of biota and environmental conditions. The final model of environmental conditions was derived by a 2 stage procedure (Pedlar et al. 1997, Schweiger et al. 1999). First, models were derived for each of 3 sets of environmental variables (abiotic environment, channel characteristics, and vegetation characteristics). Environmental variables were analyzed in 3 separate sets to better interpret the ecological meaning of each model. A forward stepwise procedure was used to create an explanatory model for each environmental variable set. Variables were selected if $P \leq 0.10$, which included more variables than would have occurred at a smaller α-level and provided a more inclusive description of relationships. Once the forward step-wise regressions were performed on each environmental variable set, the variables selected in each step-wise regression were all entered into a final backwards step-wise regression. The backwards elimination of variables removed redundant variables among the 3 data sets. Backward regression tends to be inclusive, resulting in more variables in the model than would result using forward step-wise regression. To restrict the model to the strongest variables in this final analysis, variables were retained only if $P \leq 0.05$ (unless otherwise noted). This 2-stage procedure identified predictive models for each of the 3 environmental data sets that were "inclusive" by having an α of 0.10, and then identified a final predictive model that included the strongest explanatory variables across all 3 sets of environmental variables

Potential diversity thresholds were explored through examining bivariate scatter diagrams of alpha diversity measures and environmental variables selected in final regression models. Bivariate scatter diagrams are commonly consulted in exploratory data analysis to identify potential statistical relationships (Campbell 1989, Ellison 1993). The thresholds are considered potential because their identification was not the objective of the study, but rather, they are an indication of ecological relationships that could be investigated further (Heath 1995).

Relationships between alpha diversity and environmental gradients were explored with Pearson's correlation coefficient (re: continuous environmental gradients) and ANOVA (basin orientation). These relationships provided a final look at potential environmental influences acting on alpha diversity.

Patterns of Rarity

Environmental relationships of rare versus common species were explored using the same techniques applied to alpha diversity measures (see above). In short, alpha diversity was approached by first generating descriptive statistics for each frequency variable (i.e., number of rare and common taxa and the proportion of the taxa in each group), followed by exploring Pearson's correlations between rarity and environmental variables, followed by multiple regression to describe relationships between each frequency class and the environmental variables, and concluded by an analysis of variance of changes in frequency variables by basin orientation. In addition, Pearson's correlations were explored between frequency variables and environmental gradients. All gradients were treated as continuous in this analysis.

Patterns of Beta Diversity

I used the principal components (and their associated factor scores) generated in the analysis of environmental gradients to represent the primary environmental gradients. Gradients generated through multivariate analysis are an accepted approach to defining environmental gradients for gradient analysis (e.g., Gauch 1982, Austin 1985). To more directly address relationships between biological diversity and productivity, I analyzed elevation and precipitation as individual gradients. Basin orientation was also analyzed as a gradient potentially driving changes in species composition in the basin.

The ability to quantify turnover along gradients necessitates the creation of gradient segments that can then be compared to one another. Previous studies have used various approaches to the identification of segments along gradients to facilitate the analysis of beta diversity. For example, Vazquez and Givnish (1998) used equal intervals of absolute values (e.g., 100m elevation intervals) as gradient segments in their analysis of vascular plant diversity. Alternatively, Young et al. (1998) used life zones to delineate gradient segments in their analysis of bird diversity. If sample sizes vary among designated segments, the potential bias of sample size on species composition must be reconciled, often accomplished by employing rarefaction (e.g., James and Rathbun 1981, Young et al. 1998).

The use of synthetic gradients (PCA factors) necessitated an approach to creating gradient segments that could be applied to all gradients being analyzed. I created gradient segments by dividing the 80 sample reaches into 4 equal sized segments by ordering sample reaches by their factor scores and then grouping each set of 20 sequential reaches into a group to create the 4 segments. The advantage of this approach is that each segment had an equal sample size, so richness estimates were the result of equivalent sampling effort. The disadvantage of this approach is that the range of values within a segment varied among segments. To minimize any potential biases in resulting patterns of diversity, I based the primary and secondary ranking of gradients on the sum of changes in species composition occurring between segments. Specifically, the primary ranking, "total turnover" was based on the sum of the lower of the gains or losses between each adjacent segment (i.e., 1 to 2, 2 to 3, and 3 to 4). The secondary ranking, "core turnover" was based on the sum of taxa meeting the following criteria: (1) present on more than one reach (i.e., frequency of occurrence $\geq$ 2), and (2) absent from one end of the gradient (i.e., missing from segment 1, or 1 and 2, or 3 and 4, or 4). I based the tertiary ranking of gradients on the average of the Whittaker's modified index values (β_{wMIN}) obtained from each of the 3 adjacent segment comparisons (i.e., shifts in species from segment 1 to 2, 2 to 3, and 3 to 4). The average β_{wMIN} served to represent the range in variation in beta diversity along the gradient.

Basin orientation was unique in that the "segments" (north, east, south, west) are not sequential, and there was an unequal number of reaches per orientation. For all taxonomic groups other than invertebrates, the sample sizes varied substantially among orientations: 20, 20, 16, and 24. To remove the potential sample size bias from the 3 orientations containing over 16 reaches, I randomly selected 16 reaches from the full sample of reaches, calculated frequency of occurrence values for each taxon, repeated the exercise 3 times, calculated the average frequency of occurrence for each taxon, and used those averages to represent the taxonomic composition and frequency of occurrence for the reach. For invertebrates, the 56 reaches analyzed were relatively equivalently distributed among the basin orientations (14, 14, 13, and 15 reaches per orientation), and therefore no adjustments were made for differences in sample size among orientations. Orientation was not ranked along with the other environmental gradients because it was not independent of the environmental gradients, however it was compared to the ranked gradients based on the same beta diversity measures.

Concordance Between Alpha and Beta Diversity

The correspondence of patterns of alpha and beta diversity was investigated with the intent of understanding the influence of environmental gradients on gamma diversity in the basin, and the individual contributions made by alpha and beta diversity. The interrelationships of measures of alpha diversity were explored first by examining Pearson's correlation coefficients. This step helped identify the environmental influences masked by using total richness alone as the measure of alpha diversity.

A composite assessment of alpha and beta diversity for each gradient was developed by adding total turnover along the gradient (beta diversity) to the absolute value of the sum of gains and losses in richness across adjacent segment comparisons (alpha diversity). For example, if segment 1 has 10 species and segment 2 has 20 species, and together they have 25 species, then as one moves from segment 1 to segment 2, the change in diversity attributed to alpha diversity (richness) is 10, and to beta diversity (turnover) is 5. This calculation is repeated for comparisons of segment 2 and 3, and 3 and 4. The sum of turnovers is the beta diversity element, and the absolute value of the sum of changes in richness is the alpha diversity element. The absolute value for alpha diversity was used because it represents changes in richness along the gradient regardless of the direction one moves along it (low to high or high to low). The sum of changes in richness (alpha) and turnover (beta) was used as an index of the contribution of each gradient to the overall diversity (gamma) of the basin.

INTER-YEAR VARIATION

Inter-year differences were explored by comparing the taxonomic richness and composition described by each of several sampling methods. Calculations of taxonomic richness and comparisons of taxonomic richness and composition were accomplished with a variety of methods. Statistical analysis for the comparison of inter-year variation were simplified compared to the that applied to the full data set. Inter-year variation was not a primary question in this study, but rather an important consideration in the analysis and interpretation of data. All tests of significance were set at $P \leq 0.05$.

Data Analysis

The richness and composition of taxonomic groups were analyzed relative to each sampling method. Point count data were used to describe the birds. Pitfall data were one source of information on the richness and composition of invertebrates. No pitfall data existed for McFaul 3 visit 1 in 1995, so visit 2 was used for all McFaul 3 comparisons of taxonomic richness (except visit comparisons). McFaul 3 was dropped from visit comparisons. Sweepnet data provided additional information in invertebrates, and were analyzed separately from pitfall data. Finally, riparian search data provided information on 4 taxonomic groups: vertebrates, invertebrates, plants, and fungi (Table 10).

Taxonomic richness (number of unique taxa) was used to represent the diversity of each taxonomic group, however taxonomic composition was represented by different taxonomic levels among groups. Vertebrate composition (including birds and mammals) was represented at the species level, with the exception of the following genera and families: genera = *Canis*, *Picoides* and *Sphyrapicus*; families = Accipitridae, Geomidae, and Trochilidae. Invertebrates composition was represented at the family level. Vascular plant composition was represented at the species level. Fungi composition was represented at the genus level.

A paired-t test was used to compare taxonomic richness between years. To reduce the probability of a type-I error, I adjusted the alpha level for multiple unplanned tests (where they were used) with the Tukey's method (Neter et al. 1990, p. 164).

TABLE 10. Taxonomic specificity and context used for interpreting taxonomic similarity between reaches, visits, and years for each data set and taxonomic group. All data sets using the species level include a few genera and families.

Search Method/ Taxonomic Group	Data Used for Taxonomic Richness	Data Used for Taxonomic Composition	Context for Taxonomic Similarity
Point count – *Birds*	All unique taxa	Species	Reaches
Pitfall Trap – *Invertebrates*	All unique taxa	Families	Visits and reaches
Sweepnet - *Invertebrates*	All unique taxa	Families	Visits and reaches
Riparian Search – *Vertebrates*	All unique taxa	Species	Visits and reaches
Riparian Search – *Invertebrates*	All unique taxa	Families	Visits and reaches
Riparian Search – *Plants*	All unique taxa	Species	Visits and reaches
Riparian Search – *Fungi*	All unique taxa	Genera	Visits and reaches

Sorenson's Similarity Index was used to assess differences in composition between years (Magurran 1988:95, Krebs 1989:295). This index is based on presence-absence data. The basic data for calculating the index consist of 3 values: number of taxa shared, and number of taxa unique to each of 2 sites. Sorenson's Similarity Index weights the species shared more heavily than unique taxa ($S = 2a / (2a+b+c)$), it is widely used, and performs well even if many species present at each site are not represented in the data set (Magurran 1988). Similarity indices enable the comparison of a wide range of taxa among sample reaches, but their limitation is that the similarity value is only a relative value, and needs some context for ecological interpretation.

For each data set and taxonomic group, Sorensen's Similarity Index value was calculated for each of the 8 reaches, yielding 8 similarity values for each comparison. Variation between years is of concern if it somehow biases patterns of association with spatial or environmental variables. Thus, variation between years is of consequence only if it is greater or somehow differs relative to variation from other sources (e.g., spatial variation, within-year temporal variation). To provide some measure of other sources of variation, similarities between visits and between random reach pairings within a year were calculated. Between visit similarity provided a measure of within-year variation, whereas between reach similarity reflected a level of similarity to be expected at random. The similarity of randomly paired reaches was calculated for all data sets based on visit 1 in 1995. Average similarity values were statistically compared to each other using independent sample, unequal variance *t*-tests (Sokal and Rohlf 1981).

Results

Point Count Sampling

Species richness across the 8 reaches ranged from 20 to 45 ($\bar{x}$ = 32.0, s.e. = 2.73) in 1995 and from 21 to 41 ($\bar{x}$ = 31.6, s.e. = 2.69) in 1996, with the difference between years across reaches ranging from 1-6 species (Table 11). Bird species richness between years was not significantly ($\nu = 7$, $t = 0.25$, $P = 0.813$) different.

TABLE 11. Bird species richness (S) for each sample year (1995, 1996) for 8 sample reaches based on point count data from the Lake Tahoe basin.

Reach	S (1995)	S (1996)	Difference Between Years
Burton 4	36	37	1
Griff 4	34	28	6
McFaul 3	35	41	6
Meeks 4	24	24	0
Saxon 4	33	28	5
Slaughterhouse 1	45	41	4
Third 4	20	21	1
Ward 2	29	33	4

Sorensen's Similarity Index values ranged from 0.683 to 0.814 between years (Appendix 12). The average of similarity value between reaches (0.678) was lower than the average value between years (0.762), but they were not significantly different ($\nu = 13$, $t = 2.17$, $P = 0.053$).

Pitfall Trap Sampling

Between year comparisons of taxonomic richness showed 1996 had higher richness than 1995 ($\nu = 7$, $t = 4.99$, $P = 0.002$) (Table 12). However, the between visit comparison showed visit 2 had higher richness than visit 1 in 1995 ($\nu = 6$, $t = 2.15$, $P = 0.04$). This suggests that invertebrate fauna are quite variable both within and between years, and the differences observed between years might as readily be attributed to within-site variation as to inter-year variation. It also suggests that increased sampling within or between years would detect additional taxa.

TABLE 12. Invertebrate taxonomic richness (S) for each visit in 1995 and 1996. Missing data are indicated with a dash. Between year difference represents the difference between 1995 visit 1 and 1996. Data were collected in the Lake Tahoe basin.

Reach	Between Year Difference	S 1996	S 1995, visit 1	S 1995 visit 2
Burton 4	7	31	24	20
Griff 4	25	34	9	19
McFaul 3	16	32	-	16
Meeks 4	7	23	16	18
Saxon 4	18	32	14	18
Slaughterhouse 1	3	22	19	29
Third 4	16	32	16	27
Ward 2	25	42	17	17

Sorensen's Similarity Index values between years were low, ranging from 0.263 to 0.514 between years (Appendix 13). The average similarity index value for reach comparisons was identical to the average for year comparisons (0.403), and did not differ significantly ($\nu = 13$, $t = 2.16$, $P = 0.989$). The average similarity value for visit comparisons was lower (0.366) compared to the average for year comparisons, but did not differ significantly ($\nu = 12$, $t = 2.18$, $P = 0.655$). These results indicate that although similarity between years was low, it was not lower than between reaches or visits.

Sweepnet Sampling

Invertebrate taxonomic richness was different between years ($\nu = 7$, $t = 2.86$, $P = 0.024$), with 1996 having higher richness (Table 13). However, taxonomic richness also differed between visits ($\nu = 7$, $t = 3.84$, $P = 0.006$), with visit 3 having higher richness. To best match the phenology of invertebrate life cycles between years, I selected the visit in 1995 that was closest in date to the one visit conducted in 1996. This assumes that the timing of invertebrate phenology was similar between years, which may not have been the case. The results of the analysis suggest that invertebrate fauna are quite variable both within and between years, and the differences observed between years might as readily be attributed to within-site variation as to inter-year variation. It also suggests that increased sampling within or between years could detect additional families.

TABLE 13. Invertebrate taxonomic richness for each visit to each reach sampled in 1995 and 1996, based on sweepnet data from the Lake Tahoe basin. Taxonomic richness is calculated for the 1995 visit that corresponds most closely to sample date in 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1995, closest date	S 1996, visit 1
Burton 4	24	31	31	44
Griff 4	3	13	3	12
McFaul 3	11	11	11	16
Meeks 4	7	11	11	12
Saxon 4	6	21	6	6
Slaughterhouse 1	15	37	15	34
Third 4	7	14	14	13
Ward 2	3	24	24	37
Average	*9.5*	*20.3*	*14.4*	*21.8*

Sorensen's Similarity index values between years were low, ranging from 0.148 to 0.519 (Appendix 14). The average similarity value between reaches (0.177) was lower than the average between years (0.309), but they did not differ significantly ($\nu = 14$, $t = 2.15$, $P = 0.170$). Likewise, average similarity value between visits (0.215) was slightly lower than the average between years, but they did not differ significantly ($\nu = 14$, $t = 2.15$, $P = 0.340$). The results of the analysis suggest that invertebrate fauna are quite variable both within and between years, and the differences observed between years might as readily be attributed to within-site variation as to inter-year variation. It also suggests that increased sampling within or between years could detect additional taxa.

Riparian Searches for Vertebrates

Birds comprised an average of 84% of all vertebrate taxa. Vertebrate taxonomic richness was not different between years ($\nu = 7$, $t = 2.15$, $P = 0.977$) (Table 14). However, taxonomic richness did differ between visits ($\nu = 7$, $t = 4.63$, $P = 0.002$), with visit 1 having higher richness.

TABLE 14. Taxonomic richness (S) of all vertebrates detected during riparian searches in the Lake Tahoe basin for each visit in each year, 1995 to 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1995, closest date	S 1996, visit 1
Burton 4	21	16	16	25
Griff 4	17	7	17	19
McFaul 3	32	18	32	21
Meeks 4	14	9	9	9
Saxon 4	20	12	20	17
Slaughterhouse 1	28	23	28	28
Third 4	10	8	8	8
Ward 2	30	27	27	29

Sorensen's Similarity Index values were close to 50%, ranging from 0.444 to 0.655 (Appendix 15). The average similarity value between reaches (0.450) was lower than that between years (0.564), but they did not differ significantly ($\nu = 12$, $t = 2.18$, $P = 0.059$). Likewise, average similarity value between visits (0.490) was slightly lower than the average between years, but they did not differ significantly ($\nu = 14$, $t = 2.15$, $P = 0.115$).

Riparian Searches for Invertebrates

Taxonomic richness was significantly different between years ($\nu = 7$, $t = 3.01$, $P = 0.019$), with 1996 having greater richness (Table 15). Taxonomic richness did not differ between visits, however ($\nu = 7$, $t = 2.36$, $P = 0.282$).

TABLE 15. Invertebrate family richness for each visit to each reach sampled in 1995 and 1996 based on riparian search data from the Lake Tahoe basin. Family richness is also shown for those visits in 1995 that were closest in month and day to the visit in 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1995, closest date	S 1996, visit 1
Burton 4	15	16	16	23
Griff 4	7	8	7	11
McFaul 3	10	9	10	10
Meeks 4	6	2	2	12
Saxon 4	5	11	5	14
Slaughterhouse 1	3	9	3	19
Third 4	11	12	12	9
Ward 2	5	6	6	14

Sorensen's Similarity Index values ranged from 0.118 to 0.667 (Appendix 15). The average similarity value between reaches (0.423) was higher than the average between years (0.382), but they did not differ significantly ($\nu = 14$, $t = 2.15$, $P = 0.690$). In contrast, average similarity value between visits (0.295) was lower than the average value between years, but they did not differ significantly ($\nu = 14$, $t = 2.15$, $P = 0.385$).

Riparian Searches for Plants

Taxonomic richness of plants did not differ significantly between years ($\nu = 7$, $t = 2.65$, $P = 0.498$) (Table 16). However, taxonomic richness did differ significantly between visits ($\nu = 7$, $t = 2.65$, $P = 0.033$), with visit 2 having greater richness.

TABLE 16. Plant taxonomic richness (S) for each sample year (1995, 1996) and visit (1, 2) based on riparian search data from the Lake Tahoe basin.

Reach	S 1995, visit 1	S 1995, visit 2	S 1995, closest date	S 1996
Burton 4	66	82	82	83
Griff 4	43	60	43	54
McFaul 3	52	56	52	43
Meeks 4	33	36	36	47
Saxon 4	41	43	41	45
Slaughterhouse 1	50	44	50	44
Third 4	44	57	57	49
Ward 2	50	61	61	76

Sorensen's Similarity Index values between years ranged from 0.500 to 0.709 (Appendix 17). The average similarity value between years (0.606) was almost twice as high as the average similarity value between reaches (0.353), and they were significantly different ($\nu = 14$, $t = 2.15$, $P < 0.001$). The average similarity value between visits (0.585) was close in value to average value between years, and they were not significantly different ($\nu = 14$, $t = 2.15$, $P = 0.507$).

Riparian Searches for Fungi

Taxonomic richness did not differ statistically between years ($\nu = 7$, $t = 2.36$, $P = 0.101$) or between visits ($\nu = 7$, $t = 2.36$, $P = 0.844$) (Table 17).

TABLE 17. Taxonomic richness (S) of fungi based on riparian search data from the Lake Tahoe basin, 1995 to 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1995, closest dates to 1996	S 1996, visit 1
Burton 4	7	9	9	17
Griff 4	5	7	5	6
McFaul 3	17	15	17	17
Meeks 4	8	9	9	15
Saxon 4	12	10	12	11
Slaughterhouse 1	6	6	6	8
Third 4	5	5	5	5
Ward 2	5	3	3	4

Sorensen's Similarity Index values were all less than 50%, ranging from 0 to 0.480 among reaches (Appendix 18). The average similarity value between years (0.226) was lower than the average value between reaches (0.437), and they were statistically different ($\nu = 14$, $t = 2.87$, $P = 0.012$). The average similarity value between visits (0.552) was higher than the average value between years, and they were statistically different ($\nu = 7$, $t = 3.98$, $P = 0.001$).

All Invertebrate Data

When all 3 data sets on invertebrate composition were combined, taxonomic richness was again significantly different between years when 1996 was compared to either visit 1 ($\nu = 7$, $t = 7.58$, $P < 0.001$), or visit 2 ($\nu = 7$, $t = 3.76$, $P = 0.007$) in 1995 (Table 18). The same pattern of richness between years held for family richness (Table 19). Invertebrate family richness was

different in 1996 compared to visit 1 ($\nu = 7$, $t = 7.16$, $P < 0.001$) or visit 2 ($\nu = 7$, $t = 2.92$ $P = 0.022$) in 1995.

TABLE 18. Taxonomic richness (S) of all invertebrates detected from sweepnets, pitfall traps, and riparian searches on 8 reaches in the Lake Tahoe basin, 1995 to 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1996
Burton 4	59	61	80
Griff 4	21	40	60
McFaul 3	27	35	55
Meeks 4	29	34	44
Saxon 4	28	44	48
Slaughterhouse 1	41	72	70
Third 4	32	44	51
Ward 2	33	49	76

TABLE 19. Family richness (S) of all invertebrates detected from sweepnets, pitfall traps, and riparian searches on 8 reaches in the Lake Tahoe basin, 1995 to 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1996
Burton 4	40	48	65
Griff 4	12	30	41
McFaul 3	20	22	41
Meeks 4	21	25	33
Saxon 4	19	34	34
Slaughterhouse 1	34	57	54
Third 4	21	39	41
Ward 2	18	39	59

Members of the order Lepidoptera were examined separately, and the taxonomic richness of Lepidopterans was significantly different in 1996 compared to visit 1 ($\nu = 7$, $t = 2.18$, $P = 0.027$), but was not significantly different than visit 2 ($\nu = 7$, $t = 2.14$, $P = 0.130$) in 1995 (Table 20).

TABLE 20. Taxonomic richness (S) of all Lepidopterans detected from sweepnets, pitfall traps, and riparian searches on 8 reaches in the Lake Tahoe basin, 1995 to 1996.

Reach	S 1995, visit 1	S 1995, visit 2	S 1996
Burton 4	4	5	4
Griff 4	4	5	8
McFaul 3	2	3	6
Meeks 4	4	2	3
Saxon 4	1	3	5
Slaughterhouse 1	2	6	6
Third 4	3	3	3
Ward 2	4	1	4

In summary, all 3 data sets for invertebrates exhibited similar patterns of inter-year differences. For pitfall trap, sweepnet, and riparian search data, invertebrate family richness was significantly different in 1996 than 1995, with 1996 appearing to have higher richness. For pitfall

trap and sweepnet data, the 2 visits in 1995 were also significantly different, with visit 2 appearing to have greater family richness. Riparian search data did not show a significant difference in family richness between visits in 1995. Family composition comparisons showed that inter-year similarity index was higher for all data sets, although none of the differences were significant.

Discussion

Most comparisons of inter-year variation showed no significant differences. Data sets showing no significant differences were combined across years and analyzed without consideration of the year in which the sample was taken. Inter-year variation was observed for invertebrates and fungi.

High inter-year variation in richness and composition was observed for the invertebrates. Invertebrate richness was consistently greater in 1996 compared to 1995 in all 3 data sets and when the 3 data sets were combined for each reach. The apparent under sampling of invertebrates could not be mitigated by combining all 3 data sets. Two analysis options existed for contending with the inter-year variation. One analysis option was to ensure that sample years be equitably represented in reach descriptions and comparisons. As such, inter-year variation would increase within-group variation, and make any comparison of groups more conservative. However, it would be improbable for years to be equitably distributed across every environmental variable analyzed. The other analysis option, which I chose, was to select one year to assess patterns of diversity. I chose to select data collected in 1996 because sites were selected in the same manner each year, but a greater number of sites were sampled in 1996 (n = 56) than 1995 (n = 32).

Inter-year variation was also observed for fungi. No difference in richness was observed between years, but similarity in composition was low. It is most likely that inter-year differences were the result of spatial variability as opposed to temporal variability based on the following: (1) only one sampling method was used to detect fungi (riparian searches); (2) the intensive search plots were placed in a different location in each year; (3) richness values were not significantly different between years; and (4) the occurrence of macrofungi is quite spatially and temporally variable because of their diverse life history strategies (Dix and Webster 1995). Spatial variability represents potential under-sampling of fungi relative to their diversity on each reach. I chose to use both years in the data set on the basis that more sites should represent more fully the diversity of fungi across reaches, and that variability in the data set will simply make tests of differences among reaches more conservative.